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Foreword

Until comparatively recent times the word exotic has generally been associated with alluring, fascinating, glamorous or mysterious, rather than with 'not native to the place where found'. Indeed, the establishment of botanic gardens and zoos with their many exotic species has long given respectability to the introduction of non-native organisms. However, there is a rapidly growing recognition of the magnitude of the problems that introduced species often pose. As a result 'exotic' now has threatening overtones to many and particularly to those concerned with the environment.

It is not surprising that Australian aborigines were hunters and gatherers, since so few of our native plants are suited to agriculture. The only significant food plant Australia has contributed to world agriculture is the macadamia nut. Today's human population could not be maintained without the introduction that has taken place of a wide range of exotic plants, together with a few of the exotic vertebrates. Yet, all of these—and many of the accompanying exotic invertebrates—have brought about irreversible (and sometimes highly damaging) changes in our environment: changes both in long term sustainability of agricultural production and by elimination of species, either completely or over vast tracts of country.

The introduction of exotic plants and animals, without the key organisms that regulate (or balance) their numbers where they evolved, has frequently led to their increase to past levels. The balance can sometimes be restored by classical biological control—the introduction of the missing natural enemies (often insects), when tests show that it is safe to do so. Other insects have arrived unaided or with inadvertent human assistance: many of these have become important pests.

Dr Tim New's **Exotic Insects in Australia** provides a timely overview of the current situation and will serve as a valuable background for deciding upon action to diminish present disadvantages due to exotic insects. It should also help to avoid some past mistakes.

D.F. Waterhouse
Canberra

December 1993

Preface

The traditional images of Australia range from those of its natural and magnificent native biota and landscapes to those dominated by introduced animals and plants. The latter, such as vast flocks of sheep, herds of cattle, or pine plantations, attest to both the country's prosperity and the pervasive influence and importance of animals and plants imported by Europeans during the last 200 years. Many such species are the foundation of Australia's agricultural economy. Others are pests, causing immense damage as invasive weeds, or by eating or otherwise damaging crops, livestock or other commodities. Still others have been imported deliberately to help control these pests. The history of destruction and invasion by some such introduced species, such as the rabbit or prickly pear (a cactus), has been documented extensively, and countering them is part of the history of recent endeavour to protect Australia's natural environments from such harmful organisms. Many invaders, though, have not been documented to any great extent, and their roles in the Australian environment are thus not as clear.

This short book is about one of the less conspicuous groups of exotic animals in Australia, the insects. It brings together some of the scattered information available to indicate the wide variety of effects and practical importance they manifest. My aim is to demonstrate that the numerically minor exotic insect fauna of Australia is highly significant and cannot be neglected by those concerned primarily with native species but wishing to obtain a balanced view of our fauna.

Australia, as an island continent with a long history of isolation from most of the rest of the world but subjected to massive invasion by exotic species over only the last 200 years, provides a unique suite of situations to study the effects of these intruders. On the one hand, the 'island' emphasis enables biological comparison with the greater degree of documentation on invasions of small isolated islands (such as Hawaii). These invasions have been instrumental in leading to general principles of island biogeography and understanding key aspects of the dynamics of natural communities. On the other hand, the large land area allows us to consider continental systems, which are commonly assumed to be much more resistant to invasions. The topic of biological invasions has great practical and fundamental importance in contexts ranging from planning and management of human settlements, and control of pests and disease, to conserving natural ecosystems and biota of unique evolutionary significance. Some of these contexts, and the more general biological background and principles involved, are exemplified here from the exotic insects of Australia.

Rather than 'catalogue' the numerous species involved, I have selected instances to demonstrate a wide range of contexts and concerns, and to exemplify areas of current interest and research at a time when conservation of natural biodiversity is becoming a powerful political theme in many parts of the world and when more people than ever before are becoming concerned about destruction and alienation of natural environments. 'Exotic species', generally, are one of the major threats to native biota in many parts of the world. Effects of, for example, generalist vertebrate predators, such as foxes and feral cats, are substantial in Australia—several small marsupial species have their demise attributed directly to such animals—and the effects of introduced vertebrates as pervasive grazers on vegetation are unambiguous as well. The less obvious, though perhaps equally destructive influences of exotic invertebrates need much fuller investigation. I hope that this account will stimulate awareness of some of these species and the need for careful consideration before others are introduced deliberately into Australia.

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T.R. New
Melbourne

June 1993

Chapter 1

Introduction
Exotic Insects in Australia

The long biological isolation of Australia ended abruptly in 1788 when, for the first time, animals and plants arrived in the country directly from northern temperate regions without having to contend with tropical environments on their way. Sheltered in ships' holds and cargo during their journey, they were thus compatible with their new environment and, as European settlement proceeded to create the surroundings in which they could function naturally, climatic preadaptation assured their ability to establish and—in many instance—to thrive and spread. Much of Australia's prosperity is due directly to such 'exotic' animals and plants, 'new Australians' forming a biotic component which continues to diversify as opportunities for rapid transport proliferate and suitable environments become even more extensive.

Transport was inevitably slow in those early days. The First Fleet took 35 weeks to travel from England to Sydney, via Rio de Janeiro and Cape Town, but this time had halved by about forty years later. Once the Suez Canal was opened (1869), passage times were reduced to around fifty days and, eventually, to about a month—still a far cry from modern aircraft journey times. For the first century or so, imported organisms tended to be those closely associated with people and were nurtured carefully on their journeys from the northern hemisphere, or were stowaways with an ability to exploit cargo for their well-being (rats) or with some quiescent or resistant stage in their life cycle. This situation has changed dramatically. Nowadays, an organism can enter an open aircraft at any of a large number of places throughout the world and leave it only a few hours later in Australia.

'Exotic' animals or plants are not, necessarily, strikingly unusual or vividly coloured. In biological parlance, the term is used simply to imply that they have arrived in, or been introduced to, a part of the world in which they did not evolve or where they do not occur naturally. Generally, this implies recent, sometimes historically documented, changes in geographical range and does not include those ancient invasions which have given rise to characteristic groups of fauna or flora. We are dealing, rather, with recent biological events—in Australia necessarily over only

about 200 years—involving taxa which have usually not given rise to new species in the regions they have invaded, which are not endemic to them, and whose establishment has generally been facilitated by people and by the environmental changes they have wrought.

Many plants and animals in Australia are 'aliens' in this sense. They include a large array of plants—weeds, vegetables, fruits, forest trees, ornamentals—of European and other origins, as well as animals including many kinds of birds and mammals—such as domestic stock, major pests such as foxes and rabbits, cane toads, fish and others. Often less obvious, but commonly also of vast economic or ecological significance, is a great diversity of exotic insects and related animals. Appraising the place and significance of these exotic species in Australia reveals a great diversity of human purpose and cultural intent.

Many exotic insects are pests, often because of their depredations on the introduced crops or animals on which much of Australia's economic well-being has traditionally been founded. Others are beneficial, either directly as commodities (honeybees) or as predators or parasites, referred to collectively as 'natural enemies', of pest insects. The roles of others are by no means clear, and some do not impinge so directly on human welfare. Some are innocuous. This short book is about the biology and status of exotic insects in Australia and their influences in the Australian biological and cultural landscape during the relatively short period of European settlement. Some such insects, as we shall see, are amongst the most intensively studied organisms in Australia and will continue to be so for years to come.

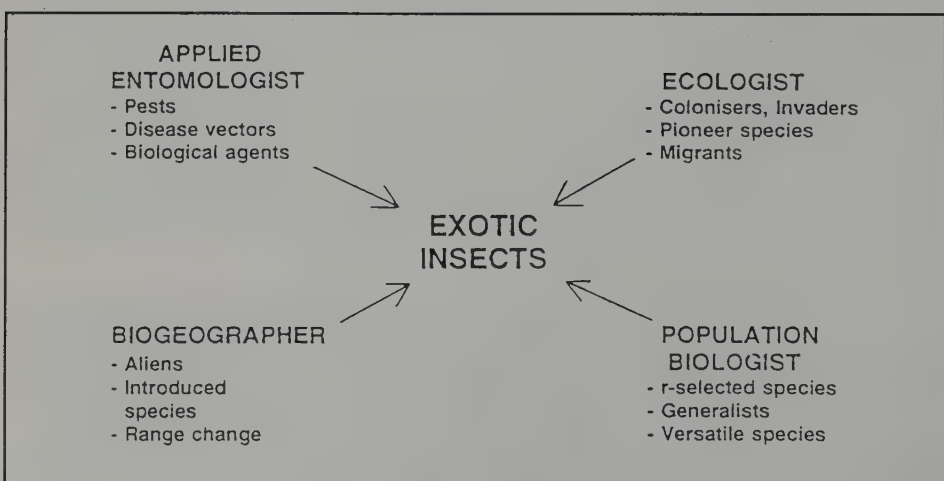

Fig. 1. Foci of interest in exotic insect species (based on Di Castri, 1990).

Much of the history of some other classic introductions to Australia (such as the rabbit; see Fenner and Ratcliffe, 1965; Rolls 1969) has been written, but, although particular insect case-histories have also been discussed in detail (papers in Kitching (1986), for example), no broad summary has been undertaken, despite the economic and ecological importance of many of the taxa involved. Understanding their biology and their actual and potential interactions both with the natural Australian biota and with the most important and damaging exotic, European humans, is a continuing and important theme in Australian ecology. Some of the major fields of interest in exotic species are indicated in Fig. 1.

The Australian insect fauna

As with mammals, birds or plants, most Australian insect species are restricted to and highly characteristic of the island continent. Great differences in climate and vegetation in various parts of the country provide an immense mosaic of environments to which such small and (often) rapidly-breeding animals can adapt. They also impose barriers to broad distribution of many because they provide an inhospitable terrain which the animals cannot colonise or cross. Very few species, as a result, occur Australia-wide, and many are highly restricted to places where they associate with particular resources (such as a given species of plant) on which they depend. Several major natural faunal groups have been delimited and recognised as native to Australia. These, discussed by Mackerras (1970), can be considered against a simple partitioning of Australia into three main 'biological regions', each subdivided extensively on parameters such as altitude, local climate, soil type or predominant vegetation.

The three divisions, proposed by Spencer (1896), take account of Australia's climatic range (from tropical to cool temperate) and rainfall regimes. A primary separation (Fig. 2) uses the 500 mm isohyet to separate the arid to semi-arid interior and far west, the *Eyrean* province, from the wetter coastal and northern fringe. Within the latter, the northern and north-eastern tropical to subtropical area is the *Torresian* province. The southern temperate parts of Australia constitute the *Bassian* province, which, on the mainland, is separated by the Nullarbor Plain into eastern and western parts. It also includes the island State of Tasmania. The boundary between Bassian and Torresian provinces is not wholly agreed, as their characteristic biota intermingle. Some characteristic Bassian insects, for example, extend far to the north, especially at higher altitudes along the Great Dividing Range, and northern taxa likewise extend southward. Thus, some 'Bassian' insects occur even in New Guinea, and a few 'Torresian' taxa reach Tasmania.

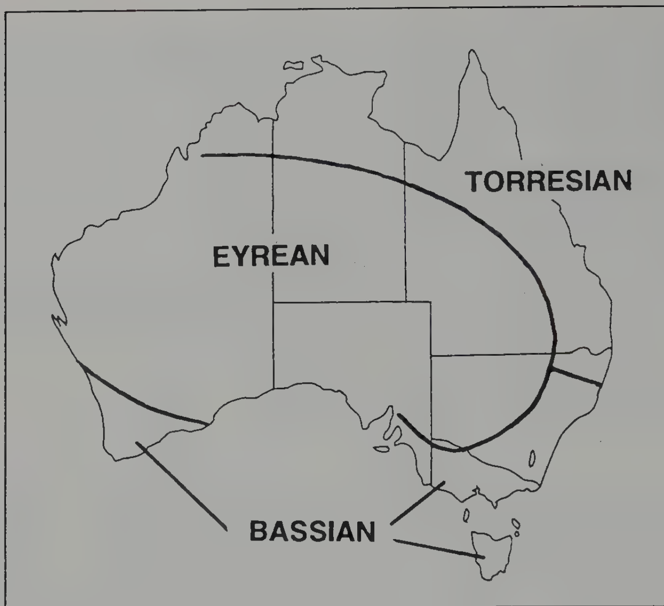

Fig. 2. Major biogeographical regions of Australia.

Evans (1959) believed that the native Australian insect fauna was derived from four elements, and the presence of these has been agreed generally. However, the first two are not always easy to distinguish, and some authorities opt to lump the third and fourth into one category. The groups are:

(1) an ancient *Archaic Element* (Mackerras, 1970). These are taxa which appear to have changed little since the Palaeozoic or Mesozoic eras and which are represented now by highly disjunct elements in different parts of the world. They are, thus, highly specialised species and often difficult to separate convincingly from the next group. It is assumed that they or their relatives have become extinct in the intervening areas where they do not now occur, so that extant forms are indeed 'relicts'.

(2) a southern or *Gondwanan element*, or *Old Southern Element*. This is a major category of native Australian insects and, in general, includes primitive groups of many orders, many of which have diversified or radiated considerably. They usually have relatives in other southern landmasses, South America, southern Africa or New Zealand, and the most frequent explanation of this is that they have been derived from the fragmentation of the former supercontinent Gondwana into its now dispersed constituent areas since the early Cretaceous.

Both of the above groups are particularly well represented in the Bassian province and, to some extent, in the northern humid regions.

(3) an *older Northern element*. This comprises predominantly ancient groups of insects which now have a northern distribution in Australia. These tend to be related to insects of Africa or the Indian subcontinent but have diversified substantially in Australia, implying that they have long been present.

(4) a *younger Northern element* (*Oriental*, *Indo-Malayan*) has entered Australia relatively recently and has strong affinities with the Oriental fauna. Speciation in Australia has been considerable but there is little diversification at the higher taxonomic levels of genus or family.

The *exotic component* is superimposed on this broad framework as a numerically minor component but one which intrudes on human consciousness far more than most native insects and one whose impact by far outweighs its diversity.

The *total* number of insect species in Australia is unknown. CSIRO (1991) noted 85,920 species in 661 families, but the true total is likely to

Table 1. Orders of insects in Australia, indicating those with exotic species and those with a wholly natural fauna. P, pests, I, innocuous, B, beneficial.

With exotic species	Without exotic species
Apterygota	
Thysanura—silverfish (P,I)	Archaeognatha
Pterygota	
Palaeoptera	
	Ephemeroptera—mayflies
	Odonata—dragonflies
Neoptera	
Blattodea—cockroaches (P)	Plecoptera—stoneflies
Isoptera—termites (P,I)	Mantodea—mantids
Dermaptera—earwigs (P,I)	Phasmatodea—stick insects[1]
Orthoptera—grasshoppers (P,I)	
Embioptera—webspinners (I)	
Psocoptera—barklice (P,I)	
Phthiraptera—lice (P,I)	
Hemiptera—aphids, scales, bugs (P,I,B)	
Thysanoptera—thrips (P,I)	
Coleoptera—beetles (P,I,B)	Megaloptera—dobsonflies
Siphonaptera—fleas (P,I,B)	Neuroptera—lacewings
Diptera—flies (P,I,B)	Strepsiptera—strepsipterans
Lepidoptera—moths, butterflies (P,I,B)	Mecoptera—scorpionflies
Hymenoptera—ants, wasps, bees (P,I,B)	Trichoptera—caddisflies

[1]Laboratory colonies of introduced stick insects have occurred, but none in the wild.

exceed this by far. A much-quoted survey by Taylor (1976) estimated 108,000 species, but even this may prove to be very conservative because of the difficulties of delimiting species solely on details of their morphology and specialists in some orders claim that a half (or, even, more) of Australian species in 'their' groups are as yet un-named or unrecognised. More than half the insect orders (Table 1) include an exotic component.

The exotic insects

All major levels of insect organisation are represented in the exotic component of Australia's fauna, from the primitive wingless Apterygota (about six species of silverfish) to the advanced winged insects with a complete metamorphosis. The great majority is terrestrial and several orders with entirely aquatic larvae (Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera) have no exotic Australian representatives, although a number of strongly-flying Odonata are widespread and Australia is part of their natural range. The other native orders mainly have rather few species, and all of the four largest insect orders (Coleoptera, Diptera, Lepidoptera, Hymenoptera) have a well-defined exotic component. Beneficial members of all of these orders have been imported as biological control agents (p. 37) but all orders (except Embioptera) with exotic species contain introduced taxa which are regarded as pests. In some, these are infrequent or have questionable status: the introduced house cricket

Table 2. Contexts in which exotic insects in Australia are regarded as pests.

Order	Context
Thysanura	Domestic
Blattodea	Domestic, stored commodities
Isoptera	Timber in service
Dermaptera	(minor) Horticultural, agricultural
Orthoptera	Agricultural
Psocoptera	Domestic, stored commodities
Phthiraptera	Livestock, medical or veterinary
Hemiptera	Horticultural, agricultural, forestry
Thysanoptera	Horticultural, agricultural, domestic
Coleoptera	Timber, stored commodities, horticultural, agricultural, forestry
Siphonaptera	Livestock, medical or veterinary
Diptera	Domestic, livestock, medical or veterinary, agricultural
Lepidoptera	Horticultural, agricultural, stored commodities
Hymenoptera	Domestic, conservation, forestry

(*Acheta domestica*) is regarded by many people as innocuous, but others see it as a nuisance. The Embioptera in Australia includes two species of an Indian genus, *Oligotoma*, which have been introduced in trade to many parts of the world, and these exemplify well the 'innocuous exotics' which scarcely intrude on human attention. The various contexts in which exotic insects are appraised as pests in Australia are summarised in Table 2.

These recent additions to the Australian fauna are generally easy to recognise and define but there are indeed some uncertainties, for a number of native Australian insects do occur elsewhere. Very few insects in Australia are naturally cosmopolitan, but some are shared with New Zealand or occur over much of the western Pacific or even further afield. It is sometimes not clear whether this is a wholly natural distribution or whether, for example, populations of northern insects in Australia presumed to be natural residents reflect, rather, frequent incursions with transient but overlapping colonisation.

Exotic insects have intruded into most of Australia, but their greatest diversity and impact is in the more intensively 'Europeanised' parts of the continent, where changes to natural environments have been greatest and where the major climatic extremes of the Eyrean province are not a barrier to establishment.

The extent of environmental change during the last 200 years in Australia has been documented broadly by many authors, some of whom have expressed concern over the continuing adverse effects on native biota. The major visual change has been the clearing of enormous areas of land, predominantly for pasture and arable farming, but also for establishment of softwood plantations (predominantly of Monterey pine, *Pinus radiata*). Forest and woodland have been most affected but, in general, much native vegetation has been replaced by exotic plant species, so that only small remnants of native species are now present in many areas. The values of 'oases' such as enclosed small pioneer cemeteries (Key, 1978) and small undisturbed areas in the Western Australia wheat belt as biological reserves for native biota have long been apparent. The cemeteries have usually been protected from grazing by stock because they have been fenced, and the wheat belt 'islands' often represent steep or stony ground unsuitable for ploughing. Both constitute remnant natural habitats in heavily altered landscapes.

The second, more localised, change to terrestrial systems has been that associated with urbanisation and the associated industrial demands of a rapidly growing human population, including development of tourist resorts along the eastern seaboard.

Matthews and Kitching (1984) referred to the areas intensively influenced by European settlement as the 'culture steppe'. This environment facilitates the establishment and well-being of insects which depend on exotic animal or plant resources, commonly those introduced deliberately as human commodities. The term 'culture steppe' refers in particular to the transformation of natural areas by deforestation so that they resemble the heavily grazed steppes of central Asia, and Matthews and Kitching expanded this European usage to include in Australia 'all parts of the landscape modified by European man directly...crop fields, improved pastures, settlements, ornamental plants, gardens and roadside', but they excluded tree monoculture crops such as orchards and forest plantations. They stressed that, after the arid region, this is the most widespread biome in Australia, and that up to about half the insect species characteristic of the culture steppe are exotic. The overall picture of much of Australia, then, is one of a dramatically altered environment, with many of the major changes having occurred rapidly and with little consideration for the conservation of native animals and plants, and with a substantial array of exotic species superimposed on natural communities, often largely replacing them. It is against this 'facilitating environment' for new arrivals, either unwanted and unheralded, or deliberately introduced, that the impacts of exotic insects must be appraised. Many of the exotic insects which we now take for granted in Australia could not persist without specific exotic resources, and must remain restricted to parts of the country where those are available readily. Others may extend more easily into natural environments. Success of establishment of any exotic species will reflect a combination of their innate or species-specific properties, the ecological conditions that they encounter, and the timing of arrival in relation to availability of resources they may need. In general, around 10 per cent of the species which arrive in a country may colonise, and only about 2–3 per cent spread widely (di Castri, 1990).

The biology of exotic species has, thus, attracted attention on many levels, but about five general questions have acted as foci for their study (Mooney and Drake, 1989). These are:

(1) How do exotic species arrive?
(2) Which species will arrive and become established?
(3) How common will they become?
(4) How far and how fast will they spread?
(5) Will they upset native communities or ecosystems?

These questions are of much more than academic interest. They relate to the likelihood of pest incidence, predictions of economic security of an insect-affected industry such as the rural sector, the need for quarantine or other preventative regulation, and the integrity and safety of the Australian natural biota and environments.

Modes of arrival

As befits the most ecologically diverse group of animals naturally dominating most of the world's terrestrial and freshwater environments, insects can often disperse actively over long distances. Conversely, they are sufficiently small or inconspicuous to be transported easily, knowingly or unwittingly, by people. Many gradations of these processes are evident in Australian examples, and some brief general comments on the ecology of insect dispersal are given below.

Aerial dispersal. Adult insects are the only winged invertebrates, and some species are regular or normal long-distance migrants. The ecology of aerial dispersal is complex, and has been investigated extensively (Southwood, 1962; Johnson, 1969; Baker, 1978; Danthanarayana, 1986; and others).

Two main processes are recognised, namely *trivial dispersal* and *migration*. Trivial dispersal involves the insect's usual day-to-day activities within its habitat, undertaken on an individual basis and without any changes in habitat—other than by accidents such as wind-gusts. Migration, termed by Johnson 'adaptive dispersal', involves all (or a proportion of) the population in a larger scale or concerted movement by which the present habitat is abandoned and a new one colonised. It is most developed in insects which occupy habitats of short duration (so-called temporary habitats: Southwood, 1962), in which resources such as suitable food may be available for only one or few generations, or for a short season each year. Migration is an integral facet of the life cycle of many insects which frequent such habitats as short-lived annual plants, or seasonal pools of water, for example, and is a vital strategy to ensure their continued well-being unless some form of dormancy can be employed for temporal escape. Spatial escape can be needed to maximise breeding time during a year, if new resources can be found thereby.

Much insect migration is over short distances, but long distance aerial dispersal is also common, and plays major roles in colonisation of new regions. In the early stages of terrestrial succession, substantial numbers of insects have been found, for example, on the bare ash or lava areas resulting from volcanic eruptions—of Mount St Helens, Washington (Edwards, 1986), and Anak Krakatau, Indonesia (Thornton *et al.*, 1988). But aerial insect populations, such as those estimated in the above studies, comprise representatives of several ecological groups.

(1) ***Strong-flying active migrants.*** Many butterflies, moths and dragonflies are vigorous flyers which tend to migrate close to the ground and can usually control the direction and distance of their movement to a large extent. Early compendia on butterflies in particular (see Williams,

1930, 1958) cite many examples of directional mass movement. In Australia, the wanderer butterfly (*Danaus plexippus*, known in North America as the monarch) is now a characteristic resident of much of the east of the country, and is occasionally recorded in the south, including Tasmania. The long-lived adults of this species in their native New World overwinter in parts of California and Mexico, whence they move northward in spring so that the species occurs over much of North America during the summer months. It was first recorded in Australia (in Brisbane, Queensland) in 1871 (Zalucki, 1986), and it is believed that it arrived naturally by 'island-hopping', perhaps aided by wind, across the Pacific. *Danaus plexippus* is well-established in Hawaii and New Zealand, as well as elsewhere in the western Pacific, and its predisposition for active flight may well have been instrumental in enabling it to reach Australia within historical time.

In general, the greatest components of the aerial fall-out we noted earlier tend to be of the following categories, rather than such strong flyers.

(2) ***Weak-flying active migrants.*** Many small or delicate insects migrate in a rather different way from the Wanderer butterfly. Aphids typically fly directly upward when they take off, and orientate actively toward blue light at that time, usually early in adult life. They thereby pass rapidly through the region of relatively calm air close to their substrate (the so-called boundary layer, defined as that region in which the insects' flight speed is greater than the wind speed and where, therefore, they can control their flight direction), into regions where they are blown by wind without any control over their destination. Such insects are then termed aerial plankton, and drift freely with their wings extended. Behaviour of many aphids changes later: they fold their wings, so that they gradually sink toward the ground. Their orientation may change to seeking green or yellow light, a change which is adaptive in finding host plants efficiently once the aphids regain the boundary layer. Such dispersal concentrates energy expenditure (energy used through flying actively) into the beginning and end of dispersal.

Both of the above processes are active adaptive dispersal modes and vast numbers of individuals can be involved. Heydeman (1967) estimated that 4.5 billion insects drift over the North Sea between Britain and the main European landmass from a 30 km coastal strip on a typical summer day, and there are other estimates of large numbers of insects over sea (Bowden and Johnson, 1976). Insect aerial plankton is high over and near all the world's tropical and temperate land masses.

(3) ***Casual or accidental aerial insects.*** Members of the taxa which normally migrate as above, together with those of many habitually

non-migrant species, may be subject to irregular events (such as sporadic strong winds) which inflict unsought dispersal on them. Thus, habitual boundary layer migrants may be blown off course, and aerial plankton removed from areas of wind convergence or from the more usual or more predictable track. Non-migrant species may be included, as stragglers, in swarms of migrants. Even events such as felling of trees may cause insects living on them to enter the aerial plankton, so that bulk samples of aerial insects (such as those obtained by suction traps, which use a powered fan to suck insects from the column of air passing over a funnel, or by nets dragged from aircraft) include both purposeful and accidental migrants.

Aerial fallout, of both living and dead insects, can be high. On Anak Krakatau, Indonesia, Thornton *et al.* (1988) recorded densities of about 20 arthropods/m^2/day, giving an approximate number of 50 million/day reaching this small island. Likewise, Edwards (1986) recorded insects of at least 70 families and 17 orders at his sites after the Mount St Helens eruption in 1980. Any or all of these are potential colonists and, although many may not have travelled far by the time they land, many others may have done so.

Distances travelled by insect migrants can be large, but are difficult to measure accurately although longevity and tolerance of insects can be adduced from laboratory studies and trials in experimental wind tunnels and other flight chambers. Collections from nets mounted on ships in the Pacific (Gressitt, 1961) or from traps on oil platforms in the Gulf of Mexico (Wolf *et al.*, 1986), as examples, indicate the presence of insects hundreds of kilometres from the nearest shore, sometimes in large numbers. Usually, it is not clear whether such insects are alive at the time of capture, but some studies using radar clearly demonstrate that a proportion of large insects (most commonly, moths) are indeed flying actively. A number of insect species seem to cross Bass Strait from mainland Australia to Tasmania, a distance of at least 350 km (Drake *et al.*, 1981), and Australian butterflies are sporadically found alive in New Zealand (Fox, 1978). Many are likely to perish *en route*, of course, but new colonising populations can indeed be based on few individuals. At the extreme, a single gravid female landing in a favourable area could be the means of establishing a new exotic species in that fauna.

Many insects migrate whilst young and reproductively immature, utilising food reserves carried over from the larval stages. Thereafter, any residual larval reserves, or energy derived from autolysis (breakdown) of the flight muscles (as in some aphids) is available for reproductive activity in the new environment, and reproduction may thus eventuate even if no food for the immigrants is found.

Most insects with winged adults could probably disperse or be dispersed (and even wingless insects are sometimes taken in aerial traps) in the air, however regularly or infrequently this may occur. Knowledge of the degree of dispersal of a given species can have considerable practical application—in formulating plans to counter or eradicate a pest, for example. A number of studies have been undertaken to determine the extent and distance of movement in insects. These may involve marking insects (for larger butterflies, with paint marks or paper labels glued to the wings; or by tagging them with radioactive isotopes) and seeking to recapture the same individuals elsewhere after they have been released. Such studies have revealed that even small insects, such as mosquitoes, can fly substantial distances: *Aedes flavescens* marked with radioactive phosphorous flew up to 10.6 km, and Horsfall (1954) recorded *A. vexans* moving up to 48.3 km. Schoof's (1959) studies showed that several domestic pest flies can easily disperse over several kilometres, and such distances may be within the range of normal trivial dispersal of strongly-flying insects. A given colony of honeybees can have a foraging range of over 300 km^2, for example (Roubik, 1989). Such relatively local dispersal is commonplace, and reflects both the propensity of such insects to become involved in longer-distance travel involving expansion or change of geographical range, and importantly, to expand distribution rapidly in a new area—such as the Australian continent—once establishment from a chance arrival has occurred (Wace, 1985).

Aquatic dispersal. 'Rafting', the dispersal of animals on floating vegetation or debris being washed ashore, has long been recognised as a possible mode of colonisation across sea barriers. It is very difficult to detect, and its role in the Australian context would appear to be small. However, the occasional arrival of insects from the north by such means cannot be discounted entirely, especially for species living in enclosed environments, such as larvae of timber beetles in trees or structural timber washed or abandoned from ships.

Human transport: insect cargo. Ships of the first fleet almost certainly conveyed insect stowaways, passengers such as cockroaches and stored-products beetles in flour or grain, to Australia, and early European settlers and imported domestic stock are likely to have been accompanied by their flea and louse parasites. Similar inadvertent introductions continue up to the present and, despite the vigilance of quarantine authorities (p. 102) are not likely to cease completely, as insects can easily be transported in ships or aircraft, free or in association with imported organic commodities. In addition, a number of insects (though, relatively few) have been introduced deliberately. Honeybees were brought from Europe in 1822 to found a honey industry, for example, and there have been recent moves to introduce leaf-cutting *Megachile* bees as pollinators

for crops in South Australia. Attempts also occurred to found a sericulture industry based on the introduced silkworm, *Bombyx mori*. But by far the predominant source of deliberately introduced insects has been the need to control pests (usually also exotic species) by importing insect predators and parasitoids to serve as biological control agents (Chapter 4).

Monkeys could be seen playing in the streets of Hobart in 1830 (Rolls, 1969); llamas and vicuna were also released in Australia in the mid-nineteenth century. Many other vertebrates were brought in during the first century of European settlement. These dramatic mammal examples are merely representatives of the numerous introduction attempts made by Acclimatisation Societies in the various States and by people over several decades before such associations were formalised. They sought to import a wide range of (especially) mammals, birds, and plants either as commodities or just to remind them of home. Many of these exotic species now constitute part of the environment which has proved so conducive to the establishment of later arrivals. Others, such as the monkeys and South American alpine mammals, failed to establish permanently in the wild in Australia. There has been no substantial insect component to the activities of those Societies. However, one aim of the Acclimatisation Society of Victoria (established in 1861), for example, included 'the introduction, acclimatisation and domestication of all innoxious animals, birds, fishes, reptiles, *insects* and vegetables, whether useful or ornamental' (my italics), so that the opportunity was indeed there for this to occur. The mid-nineteenth century social milieu which led to the formation of the Victorian Society is discussed by Gillbank (1986). In retrospect, perhaps the low number of insect species regarded specifically as commodities resulted in lack of interest in their introduction during the nineteenth century whilst the Societies flourished. Without sound quarantine measures, though, many importations of exotic plants could (and did) harbour their specific insect consumers, and animals, their ectoparasites. Likewise, seed stocks and the like may have been agencies for insect introductions from the earliest years of settlement. Importations were made from many parts of the world but with an early and natural bias towards Europe and, to some extent, North America as Australia's dependence on primary production developed.

The establishment, spread and integration, the roles of, and the concerns caused by the range of exotic insects in Australia are discussed in the following chapters. This numerically small element of our insect fauna has consistently demanded the greatest proportion of entomological effort in this country and applied entomology in Australia is founded largely on countering their intrusions on human well-being both in terms of economic and ecological impacts. These intrusions have been most intensive in the culture steppe, and are significant even in urban

environments. Attempts are now made to regulate the incidence of fresh arrivals brought through human agency, through quarantine and legal restraints (p. 102), but the chances of establishment by casual aerial arrivals continue to increase as other resources diversify. Several major pest insects occur in neighbouring countries but have not yet reached Australia—some are likely to do so within a few years, and contingency plans to counter some of these have been formulated: examples are discussed later.

Influences on establishment

In general three factors, all complex, have been suggested to as playing a part in explaining why particular exotic species establish and are successful (Spence, 1990):

i) ***Transport.*** Species which retain the ability to disperse actively may have advantages over those which are by nature more sedentary. However, many synanthropes (p. 19) may retain access to means of transport because of their regular association with goods transported by people and, once here, may be spread very easily.

ii) ***Habitat and climate suitability.*** These are perhaps the main factors which determine whether or not establishment occurs, and represent a level of 'compatibility' with the new environment.

iii) ***Biological resistance.*** Presence of competitors or natural enemies in the new environment may restrict or oppose an exotic species' potential to establish even in environments which are otherwise perfectly suitable. Conversely, if no such resistance is forthcoming—if the new species, in essence, finds an empty niche in a favourable environment—establishment and spread may be both rapid and successful.

However, the idea of such vacant niches is not accepted by all ecologists (see discussion by Herbold and Moyle, 1986), and some biological resistance is likely to be forthcoming. Most successful establishments by exotic species occur in highly disturbed habitats and, in general, establishment in an undisturbed habitat is likely to involve displacing native species by competition. The process is, thus, ecologically complex and very difficult to generalise about.

Chapter 2

Establishment and Invasion: the Milieu for Colonisation

'The invasion of ecosystems by exotic organisms represents a problem of increasing importance' (Andow *et al.*, 1990).

Topics related to biological invasions, the modes of establishment and spread of exotic species, have generated a vast literature through which two complementary questions persist. First, what are the characteristics of successful invaders, and, second, what features of a new environment render it susceptible to invasion? Many people doubt the extent to which *any* generalisations can be made on these topics, especially when comparing across major biological groups, such as plants with animals, or mammals with insects. The problems increase when attempting to predict which species may invade in the future or whether particular exotic species which are introduced deliberately (such as biological control agents, p. 37) will indeed establish and persist.

Brown (1989), discussing vertebrate invasions, showed that there was little possible generalisation even for these relatively well-studied animals. He stressed the two levels at which scientists interpret the problem. On the one hand, evolutionary biologists and ecologists commonly are content to sacrifice precision for generality in seeking to use invaders as natural experiments to understand community ecology and dynamics. On the other hand, applied biologists trying to solve specific problems cannot accept such a level of imprecision because of economic implications. The uniqueness of each species and of each invasion site may ensure that each combination must be considered as a separate case.

Many biological control programmes have shown that an agent which is spectacularly successful in one country or area may not be so in another because of different local conditions. The European cinnabar moth, *Tyria jacobaeae*, was an excellent controller of the weed ragwort (*Senecio jacobaea*) in Canada and the western USA, but failed to do so in Australia, in part because the caterpillars were attacked by native predators such as *Harpobittacus* scorpionflies (Bornemissza, 1966). Predation by native ants also apparently hindered the establishment of two European geometrid moths (*Anaitis*) brought in to control St John's wort, *Hypericum*

perforatum (Clausen, 1978). However, such clear examples of biotic resistance seem to be rather rare, and the reasons for success or failure in the establishment of exotic insects are usually not clear. There is an obvious need to monitor any such deliberate introductions closely to determine the reasons for their success or failure in any given site.

Characteristics of successful invaders

Much of the effort to characterise successful invading species has sought to define factors in common from a range of different colonisers of a new region and to contrast these features with related species which have not done so. Extreme contrasts may sometimes occur between very closely related species. Many such features were discussed for vertebrates (Ehrlich, 1989), and are summarised in Table 3. In general, many favourable features relate to the ecological breadth of a species and increasing chance of establishing from small inoculate populations. A corresponding suite of characters for plants (di Castri, 1990) gives similar correlations, but these features can be used only as a very approximate predictive guide.

Table 3. Some possible ecological correlates of good and poor invading species (after Ehrlich, 1989).

Good (successful) invaders	Poor (unsuccessful) invaders
Large native range	Small native range
Abundant in original range	Rare in original range
Vagile	Sedentary
Broad diet	Restricted diet
Short generation time	Long generation time
Ecological flexibility	Little or no ecological flexibility
Much genetic variability	Little genetic variability
Gregarious	Solitary
Female can colonise alone	Female cannot colonise alone
Larger than most related taxa	Smaller than most related taxa
Associated with humans	Not associated with humans
Wide climate/physical tolerance	Narrow climatic/physical tolerance

Many chance or accidental animal introductions start with very small populations, perhaps from single gravid females, and these may be highly vulnerable to extinction. By contrast, biological control agents may be released in substantial numbers, commonly from captive-reared stock, or in locally high densities, so that the problem of small founder groups does not exist. Otherwise, though, a very small founder population is a

bottleneck through which many prospective invaders may have to pass. It may also reflect substantial genetic impoverishment from the broad gene pool of the species in its original habitat. Small founding populations may frequently not establish, and some invading species represent the outcome of multiple arrivals, each in small numbers. Pimm (1989) emphasised that chances of extinction increase rapidly as population size decreases. (This is the basis of much of the rationale of conservation biology, where it is recognised widely that the vulnerability of a species is associated with such declining populations).

Species with a low rate of reproduction may be particularly vulnerable. For insects, a high *r* (intrinsic rate of population increase, reflecting high fecundity and reproductive rate) appears to be advantageous and, from a study on species introduced to Britain (Lawton and Brown, 1986), there was a strong negative correlation of success with body size. However, both chance and timing are critical in affecting establishment (Crawley, 1989) and the relative importance of these will vary from case to case across many aspects of population biology and ecology. Seasonal opportunity may be a critical factor for many insects which are not polyphagous, for example, and lack of any vital resource needed for establishment clearly restricts the opportunity available to that species.

In general, it seems to be easier to predict which species will **not** be successful invaders than those which will be. However, many of the failures can never be enumerated, as the arrivals have not been detected; it is generally true that an invader is noticed only after establishment has commenced. The numerous failures in deliberate introduction have, likewise, only rarely been studied to determine the reasons for this. In the past, many biological control agents have not been monitored carefully after they have been released in the field because sufficient finance or interest has not been available. Nowadays, there is much greater emphasis on assessing their environmental impact.

The receiving environment: levels of disturbance

Once an exotic species has reached a new country it has to enter not only a new geographical area but also a new biological community likely to comprise species far different from those in the area which it has left. However, such differences are becoming more blurred. A continuing trend resulting from massive human and commodity traffic is that many habitats are now more or less disturbed and their more natural biota is being replaced by rising proportions of invasive species which may predispose an area to further exotics and facilitate their establishment. More than 900 exotic plants have become naturalised in South Australia

since about 1830, for example (Kloot, 1987a,b), and each of these, in principle, could be exploited by herbivorous insects introduced from the plant's parental areas and, in turn, the specific predators of each herbivore could then invade.

Many exotic species depend entirely on disturbed habitats and do not invade more natural ecosystems. Even there, they may remain highly localised. The house cricket, *Acheta domestica*, is cosmopolitan and abundant in many parts of the world, including arid regions, but has not become widespread in Australia. Strong colonies have been reported around Adelaide, South Australia, but even there it is not generally distributed (Otte and Alexander, 1983). Other species are more aggressive invaders but, in general, only a small proportion of exotic insect species which arrive in an area may become permanent members of the new community. Most (probably, on average, more than 90 per cent species which arrive) do not establish because they do not find suitable food or other living conditions, or they encounter biological resistance from species already present. Biological resistance may be highest in more natural communities, which may be much more diverse and better-integrated than relatively simple, disturbed communities.

In addition to considering such local ecological components, attempts have been made to assess relative invasibility of different parts of the world, and it appears that northern hemisphere continental ecosystems may be more resistant to invasion than those in the southern hemisphere (di Castri, 1990, and included references). However, although establishment of exotic species may occur, it is widely held that invasion by such species does not occur without the receiving ecosystem being disturbed previously. Introduction of a new species is itself a disturbance, but di Castri suggested that ecosystems subject to irregular large-scale disturbance (such as by floods) are very susceptible to invasion, while those with low intensity disturbances are much less so.

Much discussion has taken place over the relative invasibility of islands and continental land masses since Wilson's (1965) pioneering discussion of faunal dominance based on observations that islands have received more of their species from continents than vice versa. The extent of biotic resistance is generally presumed to be higher on continents, which typically have a higher resident faunal diversity (equating to greater likelihood of competitive exclusion, and of predation and other natural enemy attack) and land area. Simberloff (1986) argued, rather, that because native insect faunas on islands tend to be small, the introduced species which become established constitute a large fraction of the total introductions. Probability of establishment did not depend primarily on what other species were already present but on the biology of the coloniser

and the availability of suitable habitat. He believed that the same species would mostly have been able to establish even in a much larger island fauna, so that continental species were in some way 'stronger' than island species.

Urban environments and synanthropy

Some kinds of insect, rather than extending widely into the Australian environment, characteristically remain closely associated with people. They are called synanthropic, a term which is broad and capable of subdivision to take account of various ecological nuances. Because of the persistent proximity between insect and human, synanthropic insects include many of the species of greatest medical and veterinary importance as vectors of disease. Exotic and native species can be synanthropic, the latter being called hemisynanthropic by Povolny (1971). Synanthropes which can complete their development in association with people and domestic stock are eusynanthropic, and examples include some virtually cosmopolitan flies (such as the housefly, *Musca domestica*) which have spread throughout the world. The housefly has a stronger association with people than, for example, the lesser housefly (*Fannia canicularis*) or some blowflies (Calliphoridae), and the latter are sometimes called exophilic eusynanthropes to contrast with the more intimate endophilic eusynanthropes. Some symbovines, such as the stable fly (*Stomoxys calcitrans*) are associated with enclosed domestic stock and others, such as the buffalo fly (*Haematobia irritans exigua*) occur with animals out-of-doors. These are all linked with humans predominantly by exploiting the faeces of domestic ruminants. Povolny (1971) also categorised separately those flies which cause myiases (p. 41).

Synanthropy can also be used in a wider sense than of maintaining close proximity to people, to mean a distribution concentrated in the culture steppe or disturbed habitats and scarcity in natural, especially climax, communities. For example, Spence (1990) appraised the carabid beetles introduced from Europe into Canada on this basis, and concluded that many were habitat generalists and not necessarily synanthropic in their area of origin. This application may be of much wider relevance.

Synanthropy, therefore, is an ecological association based on human residence. For flies, the above classification relates to (1) the food requirements of adults and larvae, and (2) the ecological requirements for other factors, such as oviposition. Perhaps the best known other synanthropes are rodents, but ectoparasites of humans could also be included as part of the extended community which depends wholly on the presence of humans. Likewise, ectoparasites of urban rats (such as the plague flea,

Xenopsylla cheopis) are sometimes regarded as synanthropic. The term is also used in a rather broader sense to include the biota which depend or can capitalise, on human habitation (some cockroaches, for example) and thus are confined largely to urban environments or occur there in much larger numbers than elsewhere. These insects are, alternatively, called domestic. Lewis (1973) delimited as domestic those insects (and other arthropods) with the habit of remaining within a man-made shelter throughout the whole or a definite part of the gonotrophic cycle and, despite its imprecision—because domesticity may be a matter of degree in a species or population—this idea is particularly useful in medical entomology. Differences between urban and rural environments also vary, and their relative definition is usually based on human population size.

A dividing level for defining urban versus rural communities of 100,000 inhabitants is often used (see Nelson, 1978), though the United Nations Bureau of Social Affairs cites 20,000, and various census bureaux may have much lower limits and sometimes declaim only 2,000–5,000 people as the lower limit for an urban community (figures from Nelson, 1978). An alternative basis for delimitation is that of economy and lifestyle: urban areas are associated with commerce and industry, and rural areas commonly with agriculture.

However, such boundaries become very blurred in both sociological and biological terms, and fringe habitats around urban centres are themselves diverse. Nelson (1978) drew a contrast between what he termed the septic fringe and the affluent fringe. The former reflects migration from rural to urban centres of people with little financial resource and is characterised by establishment of shanty towns with relatively primitive housing and rudimentary water and waste management. The latter reflects migration of upper or middle-class people away from town centres to suburbs, often involving construction of new homes or estates and large amounts of landscaping, together with full provisions for high standards of waste disposal and establishment of exotic plants in gardens. Both trends provide new resources, or a change in the balance of previously existing resources, for insects.

Anthropophagous insects constitute two main groups which intergrade: those of direct medical importance as disease vectors (p. 40) and those which may be regarded predominantly as nuisances. Tolerance to both kinds of these pests varies enormously and individually, but it has long been recognised that patterns of human settlement may be influenced by insects, particularly by presence of biting flies. Recreational resorts and development of canal-estates in Queensland include examples of such problems, compounding other facets of alienation of natural habitat for urban development. Not all the insects involved are introduced, of course,

but predominantly biting flies are commonly those regarded as cosmopolitan or domestic. Subjectivity can arise from such factors as individual susceptibility to insects (such as allergic reaction to bites or stings), but also has a socioeconomic component (Merritt and Nelson, 1978). Septic fringe inhabitants may readily tolerate higher numbers of flies than affluent fringe people, so that problems minor to the first group may assume major status to the latter. Many of the nuisance flies breed in small static water bodies or in decomposing organic matter (such as discarded tin cans and faeces, respectively) so that their population size may merely reflect availability of breeding sites. These may also have a direct bearing on disease transmission. Houseflies are mechanical transmitters of enteric disease by dispersing from faeces to human food, and Kettle (1984) likened their role to that of a pathologist's platinum loop applying a faecal sample to an agar plate for inoculation and incubation of pathogens. The house fly, *Musca domestica*, exemplifies the three ways in which a non-biting fly can transmit pathogenic microorganisms, giving it a wide range of vector potential. Pathogens can be (1) carried on the outside of the body, (2) regurgitated or vomited on to foods, or (3) deposited in the fly's faeces.

Household insects which are not of such direct pest importance also have impact in relation to the numbers present—what Olkowski *et al.* (1976) termed the aesthetic injury level, that level of abundance which offends the aesthetic values of the beholder. Tolerance levels can be influenced strongly by a person's previous background and understanding of the specific case (Piper and Frankie, 1978), so that although low numbers of insects may be acceptable, even a single individual may evince panic. It is often not appreciated that such occurrences may be no more than transient events in a clean household, and many people consider the sight of a lone cockroach or silverfish in their home a major affront to their personal hygiene standards and react (or over-react!) accordingly.

Human settlements are highly modified habitats. Agricultural and related systems included in the culture steppe are intermediate between these and natural habitats (Fig. 3), and Povolny (1971) distinguished two main categories of these. Some are highly modified by cultivation, often with exotic monoculture crops, and others are less modified and more closely resemble natural habitats. This division can be used as a basis for estimating possibilities for exchange between exotic and natural faunas by trapping regimes. Povolny suggested that exchange of species between human settlements and natural habitats was possible only for synanthropes, for example, and his main conclusions are summarised in Fig. 4. The clear implication is that habitat modification may here exclude species characteristic of less modified habitats. This is, of course, widely recognised as part of the conventional wisdom of conservation biology, but

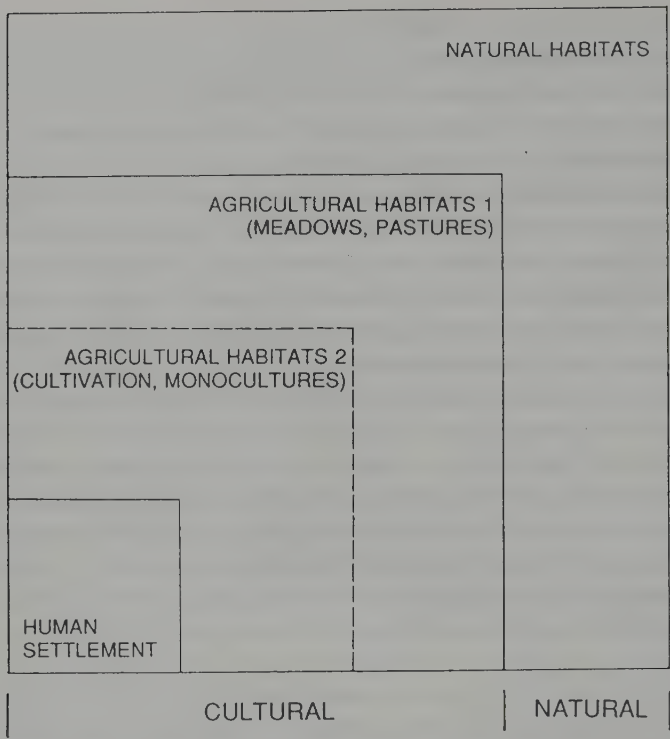

Fig. 3. Categories of habitat relevant to considering spread of exotic insects. These represent a gradient from intensively altered (human settlement) to unchanged (natural). After Povolny (1971).

particular species may adapt to such change, increase in abundance and conspicuousness in modified areas, and thereby intrude further onto human awareness. The converse is that exotic species introduced initially into human settlements may spread into less modified areas and invade natural systems. One parameter for examining the biology of exotic insects, then, is to examine their relative extents of intrusion into natural ecosystems or dependence on highly modified habitats.

In Australia, many exotic insects occur predominantly or entirely in the intermediate agricultural system, but some of these areas have been changed dramatically as they are overtaken by urban expansion. This transition has been evident around nearly all our major cities, in some only within a few decades. Much land in Australian urban areas is indeed used for non-urban purposes (Neutze, 1981). Thus, the defined urban area of Adelaide in 1957 contained more than 2,000 ha (6.8 per cent of the total) of agricultural land, slightly more (7.6 per cent) vacant land, as well as public open spaces (3.3 per cent), playing fields, golf courses, and others

where some degree of less intensive habitat modification may occur. Small areas of native or near-native vegetation in such areas are now being progressively and zealously guarded as urban reserves for conservation. Much urban expansion, though, has been into areas already substantially changed. The importance of urban gardens as reservoirs of natural diversity is also increasing in Australia, as elsewhere (D. Owen, 1978; J. Owen, 1983), especially as the trend to utilise native flora in gardens continues to replace the former emphasis on exotic ornamentals.

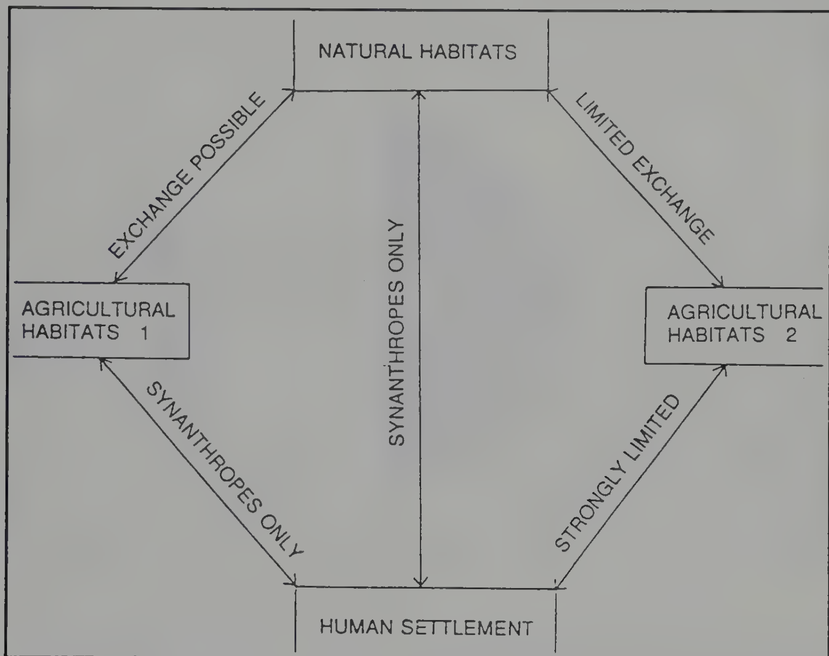

Fig. 4. Patterns of exchange of species between natural and modified habitats noted in Fig. 3. After Povolny (1971).

The typical pattern of urban expansion in Australia (Fig. 5) emphasises the presence of intermediate habitats and shows relatively well-defined population annuli around a metropolitan core population with more intensive development near the coast. Processes of urbanisation are most active on the periphery zone (Rowland, 1979) where rural land is continually absorbed into urban activity, housing, industrialisation, and services, such as airports. Populations in the intermediate zone tend to reflect local resources, but there is evidence of some recent trends, fostered in part by low prices for agricultural commodities, of some population declines. The outback, other than for local concentrations of mineral resources, tends to be settled sparsely, but very large areas are subject to

habitat change by pastoral activity or the effects of large feral mammals, in particular. Indeed, much concern over the natural environments and biota of Australia centres on the effects of such conspicuous exotic species, but the milieu of exotic environments potentially available for colonisation by exotic insects is assuredly large. How insects may then spread and establish there and elsewhere is influenced strongly by the ecology of the particular species concerned.

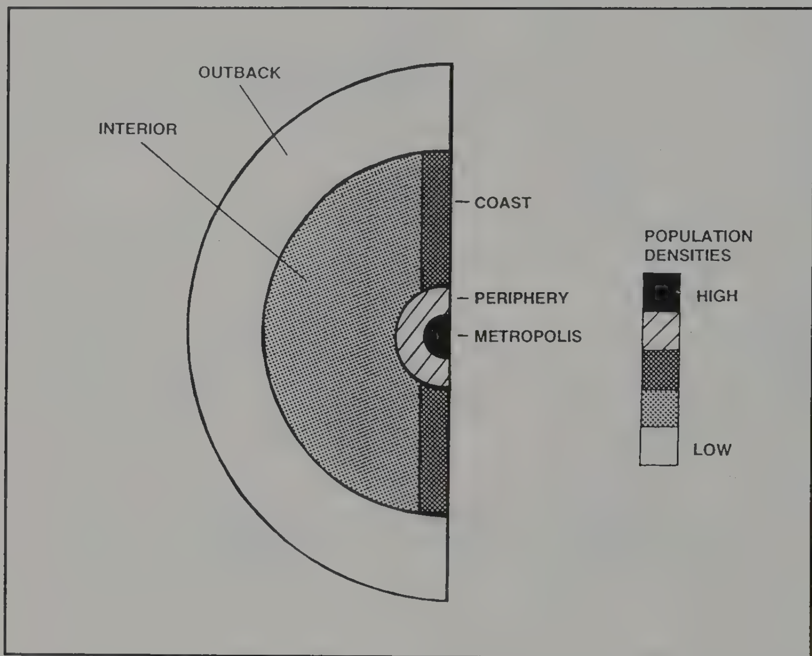

Fig. 5. Patterns of urban settlement and human population density in Australia. Schematic, after Rowland (1979).

Chapter 3

Beneficial Exotic Insects

The beneficial uses of exotic insects can be grouped into three areas for discussion: commodities, aesthetic appreciation, and for protection. This chapter initiates a discussion of these uses.

Commodities

Very few insect species have been introduced deliberately to form the basis of commodity production or industry. The most important one is the European honeybee, which has expanded into natural environments and parallels more conspicuous biota, such as certain large mammals, in having developed substantial feral populations whose size and distribution is not fully documented. The European honeybee, *Apis mellifera*, is therefore of particular significance in any appraisal of Australia's exotic insects and is at present the subject of debate between environmentalists and apiarists over its possible ecological roles here (p. 92). It exemplifies well the need for a balanced approach between the undoubted material benefits and possible adverse effects of its presence, a dichotomy which is highly unusual among insects.

Associations between people and honeybees predate historical documentation, and ancient European cave-paintings dated at around 6,000 BC show honey-gathering. It has been said that 'bee-keeping is an adaptation by man to the honeybee's biology' (Burgett *et al.*, 1978) so that, while most domestic animals have had their behaviour and biology modified to fit human needs, in contrast 'man adapts to the bee rather than adapting the bee' (Burgett *et al.*, 1978).

The honeybee was first brought to Australia, to Sydney, on the ship Isabella in 1822 (Gale, 1912). Colonies were advertised for sale in the *Government Gazette* of 21 June 1822, and the *Sydney Gazette* of 1 November 1822 included a paragraph commencing 'We congratulate our readers upon the complete establishment of that most valuable insect, the bee, in this country. During the last three weeks, three swarms of bees have been produced from two hives...near Parramatta' (Gale, 1912). Colonies were transported progressively further afield, and escaping swarms apparently formed the sources of feral populations soon after this.

The Italian bee, now the predominant race in Australia, was probably introduced first in 1862, and a number of separate importations occurred during the next twenty years or so. *A. mellifera* was introduced to Western Australia in 1846, by which time it had become widespread in the east.

In the intervening century and a half, two major benefits have accrued: a substantial domestic and export honey industry, and enhanced manipulation of bees for crop pollination. Australia has about 2,000 commercial or semi-commercial apiarists (Australian Honey Board, 1988), with honey production worth about $30 million in 1986–87. In addition, wax production exceeded $1 million but, as Hamilton (1989) noted, this is 'only the tip of the iceberg' of the industry's total worth; he cited other products such as queen bees, royal jelly and propolis, and the pollination industry. The value of the pollination industry is hard to estimate, and figures in the billions of dollars are sometimes projected. The range of $150–$400 million annually is relatively reliable, depending on market values for the crops concerned, but there are also some crops (such as almonds) which would be very marginal without honeybee pollination (Hamilton, 1989), so that the presence or availability of honeybees may determine the kind of crop which can be grown in an area, as well as its level of production. In New Zealand, all flowering crops that need insect pollination for greatest production are introduced, and the introduction of long-tongued bumble bees there for pollination of red clover (in 1885) is reported to be the first successful introduction anywhere of an insect expressly for pollination of a particular flower. Other candidate pollinator bees for New Zealand were reviewed by Donovan (1990). With the exception of *Megachile* in South Australia, which has apparently not become well-established, Australian crop pollination efforts are founded entirely on honey bees.

The tendency to become feral has ensured that honeybees now occur in many parts of Australia in this uncontrolled wild state; *A. mellifera* is an active invader of natural ecosystems, and its possible interactions with native pollinators, including the numerous species of native bees, have caused concern. This concern has been aggravated recently by the potential spread of apiary into reserved areas, such as National Parks. One consequence of the extensive clearing of eucalypt woodlands, in particular, is that some traditional nectaring sources and areas are no longer available to apiarists. There has thus been considerable competition for the remaining decreased nectar source, and pressure to extend the industry into floristically-rich reserves. Uncertainty over both the principle (of deliberately introducing exotic species into National Parks and other 'protected' areas) and the effects (harm to native pollinators through aggressive competition) has led to some vehement opposition to this (see p. 92).

A further controversy, allied with the need for resources by apiarists, has been centred on the weed (or valuable nectar plant, depending on one's point of view) *Echium plantagineum*, Paterson's Curse or Salvation Jane, recently the target of biological control programmes in Australia, a step opposed by apiarists (p. 94). The popular image of honeybees in Australia is, therefore, mixed; in addition, bees are sometimes perceived as pests in urban environments or in remote campsites where they can hamper access to water by their numbers. Many of the latter represent feral populations, and it has been implied that feral bees can also harm native birds or mammals by occupying nest holes in trees needed by parrots, for example.

In towns, bees are one of the species, which engender a fear of insects, entomophobia, but also cause concern for human safety. About 4–8 per cent of people may have an allergy to bee stings (Settipane *et al.*, 1972). There is also a nuisance component, due to deposition of unsightly faeces on laundry or vehicles.

Such pressures on the apiary industry in Australia are coming at times of decreasing financial reward. Migratory beekeeping, whereby round-the-year production is maintained by moving hives from one nectar flow to another, perhaps six or more times during a twelve month period, is a widespread need in Australia, so that loss or alienation of any one of a series of sites can have substantial effects on the livelihood of local apiarists. Because not all sites are suitable every year, a single beekeeper may need to operate from a total of around twenty distinct sites to maintain a fully productive apiary. Overwintering sites are used mainly to build up hives in preparation for the major nectar availability in spring and for pollination services. Hamilton (1979) emphasised that each State had particular resources important for beekeeping and that availability of native plants was of paramount significance; it is these very resources which have tended to decline or become unavailable. In other words, sustaining or increasing the apiary industry may need access to conserved public land, and this may be deemed incompatible with the primary use aims of these areas.

This controversy has been discussed at a number of recent conferences in Australia. The concerns raised by environmentalists collectively imply that honeybees in protected areas are incompatible with conservation (Matthews, 1984; Hopper, 1987; Pyke and Balzer, 1982; Mulette, 1986; Paton, 1993; p. 92), and are, broadly, as follows:

(1) honeybees will compete for nectar resources needed by native nectar-feeders, with the likelihood of harm resulting to these;

(2) pollination changes to native plant species may lead to changing the natural community composition by altering the relative abundance

of plant species; genetic changes through increased inbreeding or cross-breeding; inefficient pollination by nectar and pollen 'thieving';

(3) possible increased hybridisation among native plants;

(4) potential transfer of diseases to the native bee populations;

(5) spread of plant pathogens by bees and on beekeepers' vehicles; and

(6) increase in feral bee populations, and consequent competition for tree hollows used by native birds and mammals.

A policy document issued by the Federal Council of Australian Apiarists' Associations (FCAAA, 1987) recognised these as genuine concerns and, whilst acknowledging the need for research to clarify these, noted that some of the claims are erroneous. For example, FCAAA suggested that likelihood of interspecific plant hybridisation, because of honeybee foraging fidelity, is likely to be no greater than that caused by native bees, and that there is no evidence that foraging honeybees enhance the spread of fungal diseases. Several current studies seek to clarify, in particular, the first two of the above concerns, which could have far-reaching influence on the future of apiary in Australia. The central questions include whether or not nectar can be a limiting resource and, if so, whether native pollinators are indeed displaced by honeybees and suffer decrease in population density or reproductive success. Establishing this causative link is indeed complex.

There are reports of increasing scarcity of some native pollinating insects, such as jewel beetles in Western Australia, but the causes of such declines have not been clarified unambiguously. They may well relate to decrease in habitat, rather than effects of honeybees, for example. A much-quoted study by Pyke and Balzer (1982) recommended exclusions of honeybee hives from the Kosciusko National Park and other reserves with currently low levels of honeybee numbers, because of competition with native bees for floral resources there. These authors believed that such competition could be widespread and that honeybee densities in protected areas should be minimised.

Other insects deliberately introduced as commodities have not had as much economic or social impact as the honeybee, although several were originally anticipated to form the basis of substantial industries. The first deliberate introduction of an insect to Australia was a cochineal insect, *Dactylopius* sp. (Waterhouse, 1991). It was collected in South America, together with its foodplant (a prickly pear cactus, *Opuntia vulgaris*), by Philip *en route* to Australia in 1787. The insect produces a bright red dye which was to be used, as it was elsewhere, for colouring soldiers' coats. The insect species involved is not known precisely, as several closely-related species of scale insects are all known commonly as cochineal insects, but

was probably *Dactylopius ceylonicus*. Attempts to found a dye industry in Australia failed but, intriguingly, *Dactylopius* scale insects were later imported among a range of insects considered for biological control of *Opuntia* (p. 74) which had occupied some four million hectares of Queensland and New South Wales by about 1900.

Several attempts were also made to form a sericulture industry in Australia, using imported eggs of the silkworm, *Bombyx mori*. Despite vigorous advocacy, no major commercial silk production eventuated, though silk production as a hobby has continued to the present. An early booklet issued by the Silk Culture Society of New South Wales (Nisbet and Dole, undated) promoted the view that encouraging sericulture as a cottage industry could be the avenue to establishing a major industry. Attempts at larger scale silk farming were made in the 1870s in New South Wales, and Nisbet and Dole regarded establishment of the industry as patriotic work. The fervour attendant on silk establishment is exemplified by an address given to the Acclimatisation Society of Victoria by Stutzer (1864, discussed also by Rolls, 1969), in which he advocated that children in orphanages and reformatories should not waste six hours a day in education but should be put to work at sericulture, thereby overcoming the lack of cheap labour which was one of the main impediments to establishing the industry in Australia.

Aesthetic appreciation

Among the exotic insect species without direct commercial value but which are most appreciated by people in Australia, probably none surpasses the large brightly-coloured monarch (or wanderer) butterfly, *Danaus plexippus*. This species was first recorded in Australia in Brisbane around 1870 (Miskin, 1871). Its spread through the Pacific during the nineteenth century was probably largely natural: it was first recorded from Hawaii about 1841, the Caroline Islands in 1857, Tonga in 1863, and New Zealand in 1868 (although Gibbs, 1980, records possible sightings there from about 1840 on). This pattern is likely to represent a gradual dispersal. *Danaus plexippus* undertakes regular spectacular migrations in its native North America, and is reported as an occasional straggler in Europe. It may, therefore, have 'island-hopped' across the Pacific Ocean, possibly aided by human transport. Establishment in Australia was dependent on the presence of introduced milkweeds (Asclepiadaceae), some of which were introduced originally as garden ornamentals and are now widespread in the east as weeds along roadsides and creeks and on abandoned farms and cleared land. Zalucki *et al.* (1981) noted milkweed patches of up to about 20,000 m^2, and other weeds, which provide nectar for the butterflies, are often associated with these larval foodplants.

Twelve species of Asclepiadaceae, four from America and eight from Africa, have been recorded as larval foodplants in Australia (Zalucki, 1986). However, the Australian distribution of *D. plexippus* is less extensive than that of apparently suitable larval foodplants and the reasons for this are not wholly clear. The butterfly's winter range is predominantly north-eastern (Fig. 6), with overwintering areas also around Sydney, near Adelaide and (possibly) also on Philip Island, Victoria. The summer range is much more extensive, and normally includes much of the east of the continent, with more sporadic records from Tasmania. Records from various coastal sites in Western Australia and the Northern Territory may represent casual stragglers from elsewhere, but the status of any populations there (and at Alice Springs) is by no means clear. The range contracts markedly towards the coast in autumn. Winter breeding is not possible inland or in most southern areas because the milkweed plants die back there over that period.

Zalucki (1986) noted that *D. plexippus* has acquired several species of parasitoids in Australia. Milkweeds have also been adopted as foodplants by the native species *D. chrysippus*, and may thus have facilitated the spread of this species as well.

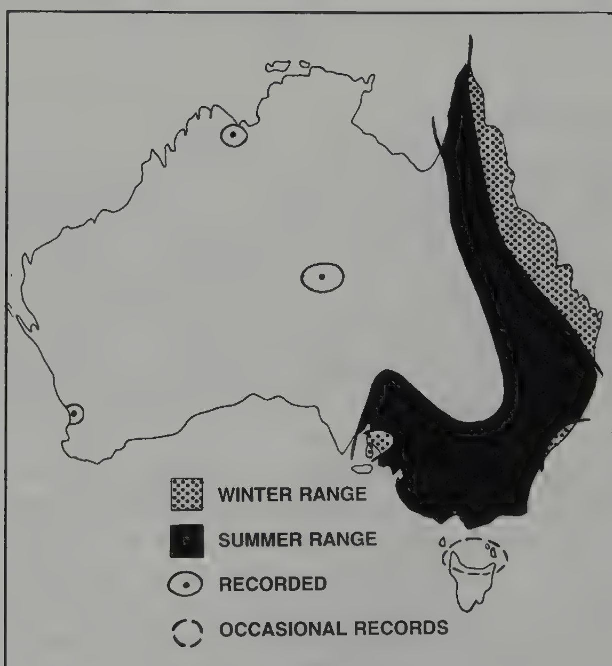

Fig. 6. Seasonal distribution patterns of the wanderer butterfly, *Danaus plexippus*, in Australia. After Zalucki (1986).

Other beneficial insects

The examples noted here, although including the most obvious beneficial insects in general public perception, neglect what is undoubtedly the most diverse and significant element of our beneficial exotic insect fauna—those numerous natural enemies of exotic pest arthropods and plant weeds which have been introduced deliberately to control pests and counter their deleterious effects. Many such insects have been, and are, of major economic significance in protecting virtually the whole range of crops and agricultural commodities. They are discussed, in a broader appraisal of pest control, in the next two chapters.

Chapter 4

Pests and Pest Control

Exotic pest insects

The few exotic insect species usually regarded as having a definite positive value as commodities to Australia are vastly outnumbered by those categorised as *pests*, in itself a rather vague term but one which implies that they cause nuisance or more clearly-defined damage to human economic or social well-being. This is often through their direct depredations on plant crops, but can also be through feeding on animals or people (sometimes acting as vectors of diseases), on stored commodities (such as grains), or on structural timbers. The culture steppe environment, as we have seen, is particularly susceptible to the damaging effects of exotic pests, and the technical literature on their biology and how they may be countered or controlled is vast. Much of the science of applied entomology in Australia is essentially synonymous with suppression of exotic pests, and this demands continuing and substantial endeavour.

The science of insect pest control has changed considerably during the last few decades and has become much more sophisticated than previously. Design of alternative control strategies to the direct use of pesticides has sometimes tested the ingenuity of entomologists to a substantial extent. Some of these strategies employed against exotic pests in Australia are discussed in this chapter to exemplify the challenges posed by these insects and how they may be met.

The status of a pest usually has a component related to pest numbers—with greater numbers enhancing damage or severity of pests. However, very few individuals may be involved. We noted earlier (p. 21) the case of a single transient cockroach, a case which exemplifies that subjectivity may play a part in how pests are perceived. Commonly, though, and especially for pests which are direct despoilers of commodities such as crops, numbers are directly important in relation to the amount of damage caused. This, in turn, determines the need for control and the investment warranted to achieve this. A simplified scheme for this (Fig. 7) evokes two levels of pest numbers, related to the normal fluctuations in population size. The *economic threshold* (e.t.) is the number of pests above which economic injury (financial damage) would occur through despoliation. The *economic injury level* (e.i.) is the minimum number of pest

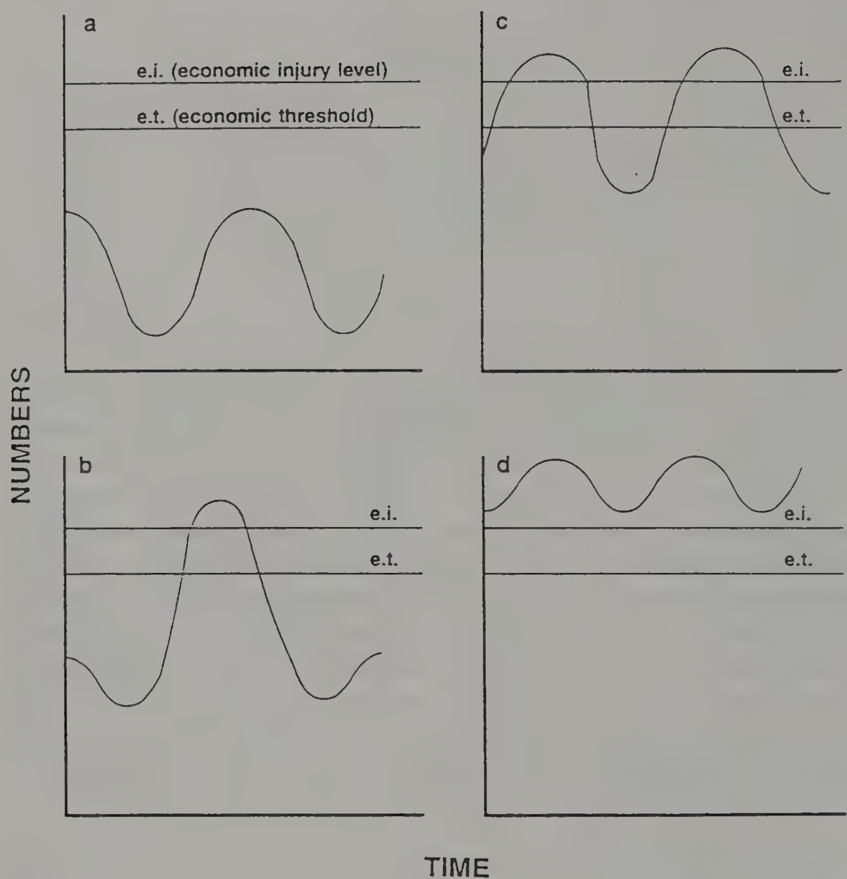

Fig. 7. Pest status in relation to numbers of insects:population sizes change with time, e.t. (economic threshold) is the level above which e.i. (economic injury) will occur, and the level at which control measures are needed. *a–d* are increasing levels of severity of pest status: *a* is innocuous, as the insect population never reaches damaging levels, *d* is permanent pest status with numbers always causing injury.

individuals which results in actual damage, that is, loss of financial return. Ideally, control measures should be implemented at, or slightly before, the economic threshold in order to prevent economic injury but, as both of these levels reflect actual or anticipated commodity prices, they may be difficult to predict and may vary substantially between years or seasons. The fundamental equation is that no more can be spent on protecting (say) a crop from pest attack than a predetermined portion of the expected returns from that crop in the market place. There is thus an over-riding economic consideration to implementing pest control and protecting economic commodities. This is universal for commercially grown crops, but perhaps particularly relevant to exotic pests attacking exotic staples or commodities which are otherwise in very short supply.

Pest intensity can also be reflected in frequency of attack. Some insects are only sporadic or occasional pests, so that crops do not suffer damage every year or every planting. Others are more regular pests, so that they are present predictably whenever their food crop is grown, and part of the anticipated costs of growing that crop is the cost of combating its consumers. Killing the pests is the most frequently-employed strategy, but others also play a part. It may be possible, for example, to evade the consequences of pest attack by growing a crop where the pest does not occur, or to alter the fate of the commodity: if orchard fruits are grown specifically for juicing, blemishes caused by codling moth, or presence of scale insects on citrus, are of little consequence. If, on the other hand, those fruit are projected for individual sale in supermarkets or for export, such symptoms would seriously diminish their market potential because they would be rejected as being of low quality by purchasers and excluded from their target market. For stored products, such as grains, or timber in service, as in buildings, preventing access of potential pests may be an important aspect of control. For biting flies and other nuisance insects, public education to alleviate the image may occur.

Pest management in urban or highly modified areas has a number of sub-fields, with different areas of concern (Olkowski *et al.*, 1978). Many of these can be budgeted in terms of cost/benefit, as exemplified above, but for some this is hard to do. In particular, two categories of exotic pest in Australia are not directly related to quantifiable commodity degradation—those 'psychological' pests affecting human comfort, which include nuisances and species which engender symptoms of hysteria (Olkowski and Olkowski, 1976); and those which invade natural systems and whose prime role may be to interfere with or displace native biota (Chapter 6). Olkowski and Olkowski (1976) included psychological pests as one of seven categories of urban pests. The others, each reflecting an area in which more direct or tangible damage can occur from insects, are:

- medical (disease vectors),
- architectural (wood feeders, textile and fibre feeders, furniture beetles, and others),
- agricultural (pests of vegetables, stored cereals, fruits and other food),
- floricultural (pests of decorative flowers or house plants),
- silvicultural (pests of trees grown for economic value, e.g. timber, christmas trees), and
- horticultural (pests of nursery and amenity plant growths, botanical gardens, roadside ornamentals).

These have overlapping components in optimal pest control strategies but also elements peculiar to each. There is a vast literature on pest

control and my approach here is to discuss, rather, the kinds of control which have been developed for a selection of exotic insect pests in Australia; it is not to provide another comprehensive account of pest control but to exemplify the economic impact of the insects and the scientific elegance needed to counter this. Together, though, the kinds of control indicate many of the current frontiers of applied entomology in Australia and summarise some of the country's impressive record of achievement in this field. Not all pest insects are exotic, of course. The termites (Isoptera) which attack structural timber, and which can become one of the most significant groups of urban/suburban pests, contain only three exotic species in Australia, all species of *Cryptotermes*, and none widespread. The vast bulk of termite damage is caused by native species. In general, the multitude of insects attacking native trees, such as *Eucalyptus* or *Acacia*, are almost wholly natives. They include some very important forestry pests, especially to *Eucalyptus* grown under plantation conditions for hardwood timber or for provision of shelter belts on farms.

Textbooks such as that by Cherrett *et al*. (1971) give abundant background and information on many facets of pest control strategies. Mortality may be imposed directly by chemical, physical or biological means, and other methods interfere with the insect's behaviour or environment and thereby hinder its reproductive success or its ability to find mates or food. The latter categories of control method are sometimes very difficult to develop to the stage where they can be used reliably on a commercial scale, and some are effective only in very limited contexts. Pest management incorporates all options available to control a given pest, and these options may differ markedly from case to case.

In the past, there has been a general presumption that any insect pest is susceptible to some kind of chemical pesticide and that most will also be amenable to control by biological means such as natural enemies. The recent history of insect pest control reveals an active transition from high reliance on pesticides to one of lowering this dependence in every possible way by substituting methods which are less damaging to the environment or less costly. Pesticides still have a vital role in modern Integrated Pest Management (IPM) and will continue to do so, but their use is now more sensitive and selective than formerly. DDT, for example, has been banned in Australia since the early 1970s and various other potent chemicals have been banned or strictly regulated in use in the intervening period. Some of these were the sole, or major, controls employed against particular pests or the pest complexes on certain crops. Problems of resistance developed by the pests gave additional practical reason for seeking alternatives, as the pesticides were then ineffective. Both social and economic pressures drive the methodology for pest management and even apparently simple relationships between pest and

commodity can be immensely complex. A single widespread pest species, a situation typified by many exotic insects, may demand different methods or intensities of control in different parts of its range or in different economic climates.

Biological control

Biological control, the use of predators, parasitoids and/or pathogens, utilises both native and exotic 'natural enemies'. The former can sometimes be encouraged or increased in abundance by cultural practices or, more predictably, by release of mass-reared laboratory stock to augment low natural populations and enhance their impact on the pest. By far the largest group of biological control agents comprises insects. The largest single category of insects introduced deliberately to Australia has been those intended to function as biological control agents—the predators and parasitoids of pest insects and the consumers of plant weeds. The early history of biological control in Australia (Wilson, 1960) lists numerous such introductions from many parts of the world. They are employed almost entirely against exotic pests, and are thus sought in the original range of the particular insect or plant pest, or in other areas where it has become naturalised or, in some cases, already been controlled successfully. It is this classical type of biological control which is our major concern here. The rationale is, typically:

(1) the pest has pest status, at least in part, because it has entered a new environment conducive to its well-being but free of its usual natural enemies;

(2) as a result, the pest lacks predominant factors which would normally oppose its population increase, so that

(3) it reaches unusually high (damaging) numbers;

(4) natural enemies have the capacity to restore the balance and reduce the pest from (or prevent it reaching) numbers sufficient to cause damage; and

(5) if they can be employed to do this, pest status is eliminated.

Introduction and establishment of suitable natural enemies therefore restores some absent elements of the pest's natural life-system, and these are recognised widely as among the most important components influencing pest numbers. Their continued presence, in association with low (non-damaging) levels of the pest may constitute a more or less permanent control by suppressing pest populations in the future. In general, introduced biological control agent insects are viewed as permanent additions to the fauna of the area in which they are liberated. However,

native pest species may also be suitable for biological control by imported natural enemies (DeBach, 1974) and this scenario occasionally generates some concern from environmentalists.

Much thought, analysis and experimentation has been devoted to defining the characters of a successful classical biological control agent and of clarifying parameters of its efficiency and safety (Huffaker *et al.*, 1971), and a number of biological control protocols have been designed either for insects attacking other arthropods or weeds. Desirable characteristics of an agent include:

(1) ability to adapt to the physical and climatic conditions of the new environment;
(2) high effectiveness in searching for prey/hosts/foodplants;
(3) high rate and extent of population increase relative to abundance of its food supply;
(4) synchronisation with the food supply so that, for example, the consumer should not become dormant at times of food abundance;
(5) feeding specificity, and
(6) ability to respond to changes in range and biology of its food species.

Of these, searching efficiency and feeding specificity have particularly far-reaching consequences. In general, parasitoids (almost wholly Hymenoptera) have been employed more frequently than predatory insects against pest arthropods. They are often more food-specific than predators and form closely adapted and biologically synchronised relationships with their insect hosts. Because parasitoids usually require only one host in which to develop, whereas predators usually need many individual prey, they can be effective at low host densities. In contrast, predators may require high prey densities in order to develop, but high voracity itself may ensure a rapid impact on the prey population. Studies on lacewings (Neuroptera, especially on Chrysopidae and Hemerobiidae) and ladybirds (Coleoptera, Coccinellidae), for example, have demonstrated that a single predator may consume many hundred individual prey (such as aphids) during its lifetime. Predators have also been used frequently, and in order to determine the most effective natural enemies for a given pest it is usually necessary to investigate a number of different possible candidates for introduction.

Many early biocontrol practitioners advocated introducing a diverse range of enemies of any pest, so that the most effective would then be determined by natural selection in the area of introduction. The converse, that only agents which have been screened intensively for safety and efficiency should be introduced, is now more generally paramount—and, in some countries, the only practicality allowed for by enabling legislation

concerned with the release of exotic species. In most cases though, several such agents are (or can be) introduced against the same pest species, and it may be extremely difficult to predict which might be the most effective or useful one (see discussion by Waage, 1990). It is often also unclear what, if any, combined or competitive effects will occur from multiple-agent introductions. Huffaker *et al.* (1971) emphasised, using examples from California, that the vast investment in prior ranking of potential agents is unnecessary, and that introduction of a sequence of relatively specific enemies is a desirable practice. Multiple introductions may counter environmental variations which influence the efficiency of any one particular agent, in that such effects might be buffered or control enhanced by another agent. There is also, usually, an urgency about any given biological control programme in that a pest needs to be controlled within a short space of time; sufficient time for the development of an ideal approach therefore may simply not be available.

The need for good searching ability, long ranked as among the most desirable features of an effective natural enemy, ensures that the agent may be able to exploit the target at low densities and track it throughout its habitat. There are numerous examples of the use of different climatic strains of an agent whereby apparently the same natural enemy species introduced from different climatic areas (see the Green Vegetable Bug, p. 72) perform differently in their new habitat. It is not always clear whether the same species really is involved among some such strains because very subtle biological features separate members of putative sibling species groups in small Hymenoptera (and other insects), but in some taxa mass-rearing in the laboratory can be used to select artificially for the most effective stocks to release. Candidate agents are indeed studied intensively before release, both to clarify their biology and ensure their feeding specificity and to determine that they will breed adequately and associate with the target pest. Feeding specificity is of critical importance in ensuring that the agent will not attack non-target organisms and has assumed particular significance in selecting agents for use against plant weeds. Any such agent must not attack crops or ornamental plants related to the weed, for example. Such extreme feeding specificity is hard to prove, especially when allowing for the untried foodplant spectrum in a new part of the world. For weed-control agents, extensive testing is undertaken routinely against likely non-target food species from the area of proposed introduction, and any possibly significant feeding side-effects are likely to result in rejection of the candidate before it is released. In general, pro-formas for testing (screening) such phytophagous insects are reasonably well-defined, so that mistakes are nowadays extremely rare. Harris (1981, 1985) pointed out the three parameters which determine whether an insect will damage a plant species: ability, opportunity, and the advantage of doing so. Ability to feed

on a given plant in the laboratory screening phase does not mean that it will necessarily do so in the field; under such confined conditions, many insects can be induced to feed on plants which they may not attack in nature. Lawton (1985) drew the analogy that starving people will eat cats, rats and shoe leather, but that information was not (he suggested) useful in predicting what he would eat for lunch!

Insects introduced into Australia against weeds such as prickly pear (p. 74), St John's wort (*Hypericum perforatum*, p. 76) or Paterson's Curse (*Echium plantagineum*, p. 97), thus, are not likely to feed and develop on desirable or non-target plant species.

Feeding specificity is of greater significance than just assuring an agent's safety, however vital that aspect may be. It often reflects a long period of coevolution, of intimate and intricate association, between the consumer and its food species, so that the consumer might be expected to respond subtly and reliably to changes in the latter's biology or abundance. Such specific feeders account for most of the outstanding practical results in classical biological control. The examples cited later in this Chapter include some very spectacular successes of classical biological control in Australia, and these have helped to enhance the image of this technique as a panacea amongst pest control methodologies. A caveat to this attitude is discussed in Chapter 6 (p. 96). Classically, a biological programme of the kind discussed above consists of several phases:

(1) exploration for candidate natural enemies;
(2) laboratory studies before release to determine safety and suitability, during which the range of possible candidates is usually narrowed substantially;
(3) release of agents in the field, and
(4) monitoring their progress in the new environment.

In the past, many releases have not been monitored perceptively, so that reasons for success or failure have not been wholly clear.

Pests of people and animals

Insects which bite or otherwise molest people or domestic animals are important in three contexts—as nuisances affecting the victims' physical or mental well-being, by inflicting direct injury or wounds (myiases), and by their ability to act as vectors for diseases, including some of the most important parasite-related diseases known. This gives them massive medical and veterinary importance and can result in enormous control campaigns. Outside Australia, control of tse-tse flies (*Glossina*), the vectors of the trypanosome causing sleeping sickness in Africa, and of

mosquitoes carrying the malaria parasite, are major examples. Mosquito vectors are a concern also in Australia, mainly now for other diseases (p. 107). Very rarely, disease vectors can be beneficial: in Europe, the rabbit flea (*Spilopsyllus cuniculi*) is the main vector of myxomatosis, and unsuccessful attempts have been made in the past to establish the flea in Australia to augment the level of disease transmission between rabbits resulting from mosquito carriage. This species is currently the subject of renewed interest as a potential myxomatosis vector in central Australia. Both native and exotic insects are involved as human or stock pests in Australia.

Many of the exotic insects involved are synanthropic and a high density of people or animals naturally increases their pest potential (Chapter 2) because hosts are readily available. Flies are by far the most important insect group involved, but ectoparasites (lice and fleas) and some blood-sucking bugs (Heteroptera) are also involved. Their natural history is discussed extensively by Busvine (1975, 1980) and Kettle (1984), amongst others.

Myiases. Larvae of some pest Diptera invade the living tissue of victims to cause wounds, or myiases. Functionally, there are three main kinds of myiasis and Kettle (1984) noted that they can also be classified clinically by the body part and tissues attacked.

The first major category is exemplified by the screwworm fly, *Chrysomya bezziana* (p. 112), which is an obligatory agent of myiases, because larvae occur only in wounds. In contrast, the sheep blowfly, *Lucilia cuprina* (below), is a facultative agent because larvae occur in wounds but the fly breeds also in carrion. This category can be separated into primary flies,which can initiate myiases,and those which participate only later and invade existing wounds. Many carrion-breeding species are such tertiary flies, invading myiases only when the host is already seriously stressed or dying. The third main category involves accidental myiases, in which, if eggs or maggots are consumed accidentally, they might survive and develop in the host intestine.

Collectively, such flies can be of vast economic importance.

Sheep blowfly. Probably, no pest insect in Australia has had more spent on studies of its biology and control than the sheep blowfly, *Lucilia cuprina*, the fly which is mainly responsible for initiating myiases in sheep. Kitching (1981) regarded it as 'one of the most widespread and pernicious pests in the whole livestock sector'. *Lucilia cuprina* is thought to have been brought to Australia from Africa, probably in the 1880s, though possibly slightly later as the first major pest-status records (in New South Wales) were not until 1897. It became widespread by the early

1900s and has been studied ever since. *Lucilia cuprina* now occurs wherever sheep are raised in Australia but is absent from the arid centre of the continent. Other flies also 'strike' sheep (Norris, 1959, listed 18 species in the families Calliphoridae, Sarcophagidae and Muscidae), but most of these are infrequent, and *L. cuprina* is by far the most important of the eight 'primary strike' species which initiate wounds later exploited by 'secondary strike' species, and which thus lead directly to infestation of skin and wool with maggots. Annual losses due to sheep blowfly may exceed $100 million. Cutaneous myiasis is thus of vast importance, and the paramount high quality wool providers, merinos, are highly susceptible to fly strike because of their folded skin. Death of the sheep often follows and survivors are in poor condition with reduced wool yield and quality.

Two main approaches to reducing the impact of fly strike have involved: (1), direct protection of the sheep, and (2), attempts to reduce fly numbers.

The first of these included development of the classic Mules operation to remove folds of skin from the susceptible breech area, augmented by regular crutching (shearing of breech wool) to reduce fouling. Moderate tail-docking helped to reduce tail-strike, and jetting or spraying sheep with insecticides also became a regular component of protection.

Most classical methods and some highly innovative developments have been investigated in attempting to reduce fly numbers: biological control (where no sufficiently rapid-breeding natural enemies were found), carcass destruction (impracticable over large areas), and trapping of adult flies (difficult to achieve in sufficiently large numbers) were all abandoned by the 1950s. Increased resistance of flies to many of the protective chemicals, such as dieldrin, organophosphates and carbamate, led to decreasing use of these because more frequent applications were needed (Foster and Whitten, 1974). Economic margins in the sheep industry can be very small and any extra cost of control may not be justifiable.

More recent emphasis, from about 1970, has been on aspects of genetic control. The two approaches, termed genetic load and genetic manipulations, are rather different in emphasis. The first essentially introduces sterility into the field population by release of sterile insects (SIRM, the Sterile Insect Release Method) every generation, or chromosomally altered strains with sterilising effects extending over several ensuing generations. The second introduces conditional lethal mutations, such as eye colour mutants which are harmless in the laboratory but which affect vision and cause early death in the field (Davidson, 1984). Early developments in these areas were reviewed by Foster *et al.* (1975) and Whitten *et al.* (1976). Reduced fertility can result from matings by flies with an abnormal compound chromosome, and introduction of harmful

genes, such as those increasing susceptibility to insecticides or to climatic extremes, have been explored progressively over the last 20 years. Research on genetics and ecology of the blowfly is paralleled by work on improvement of techniques for mass-rearing, sterilisation and release of flies (Wardhaugh *et al.*, 1983). Bacterial control methods are also being investigated.

Other introduced flies. The buffalo fly, *Haematobia irritans exigua,* was introduced into Australia on water buffalo imported from Timor in 1838 and is now widespread in tropical and subtropical regions. There is suspicion that it could spread to as far south as northern New South Wales. Both sexes are blood-feeders and larvae occur in dung. The flies can occur in high numbers (500–5,000 or more per animal) and these can result in lower weight gains for beef cattle and lower milk yield for dairy herds. It is an obligate feeder on cattle and is regarded as the most important insect pest of cattle in Australia.

The lesser housefly (*Fannia canicularis*) and the stable fly (*Stomoxys calcitrans*) are both cosmopolitan synanthropes. The latter can cause stress to stock (and people!) by its bites and is conspicuous because it is diurnal and bites especially in early morning and late afternoon. It has been reported to reduce milk yield by up to 60 per cent (Greenberg, 1973) and can be an intermediate host for several nematode worm parasites of cattle or horses. *Fannia canicularis* has been reported to cause intestinal myiasis in people, most likely because they ate fruit or vegetables.

The sheep bot fly, *Oestrus ovis*, is also widespread in Australia, but probably not very important. The female lays larvae in the nasal cavity of sheep. Maggots develop until fully grown in the frontal or maxillary sinus, whence they are evacuated by sneezing and pupate in the soil.

Gasterophilus intestinalis is the most widely distributed of the stomach bots of horses and is the predominant species in Australia; it was presumably introduced with horses. Eggs are laid on horses, mainly on the front legs, the cheeks and the intermandibular space below the jaws, and hatch when they are taken into the horse's mouth. First instar larvae burrow into the tongue's mucous membrane (Zumpt, 1965). Later instars live in the intestine and attach to the gut wall by their spined mouthparts. Heavy infestations can lead in extreme cases to death, but extensive ulceration and abcess formation is more common (Waddell, 1972).

Dermatobia hominis causes myiases in many domestic hosts, most importantly in cattle. It can infect people and cause swellings. Very rarely, *D. hominis* has been recorded penetrating the brain and causing death. It is endemic to South America and has been imported into Australia by travellers (Kettle, 1984).

Sheep keds, *Melophagus ovinus*, are common in cooler parts of Australia. This Palaearctic fly is a permanent ectoparasite of sheep and can cause loss to a wool crop by anaemia and staining of the wool by faeces. In Australia it is often referred to as the sheep tick.

The role of most flies as disease vectors is enhanced by their facility for dispersal, so that a disease may be spread a considerable distance by a fly dispersing from a food source and biting, or contaminating human foods, elsewhere. Most other insect disease vectors disperse much less readily.

Other insects of medical importance. Domestic **cockroaches** (Fig. 8) parallel synanthropic flies as vectors of disease-carrying bacteria, viruses, protozoa and helminths and, like houseflies and others, are

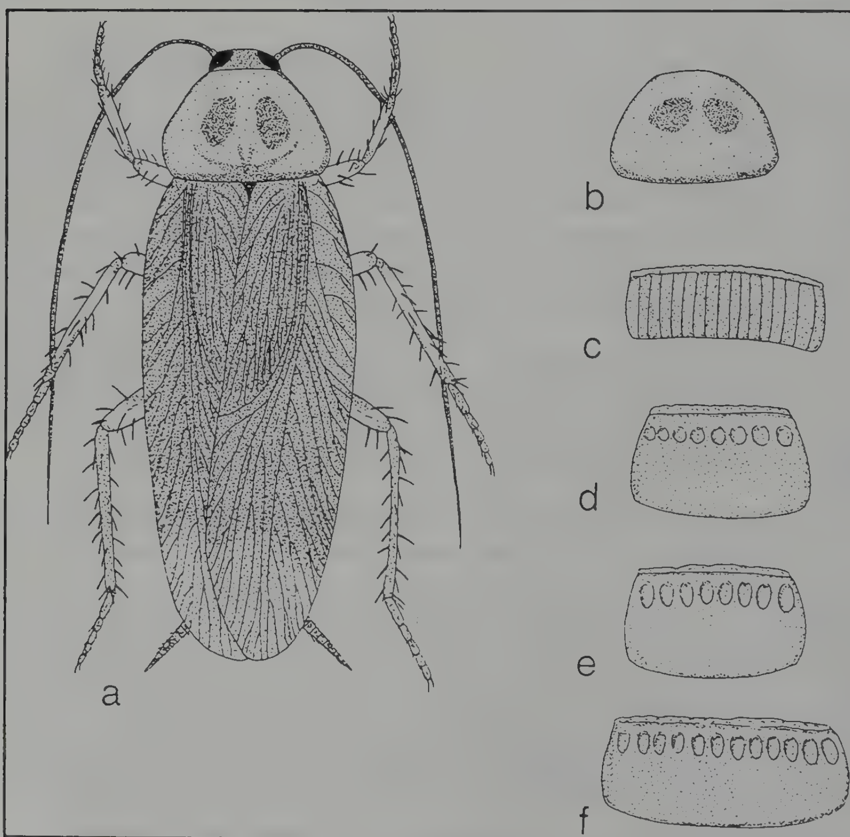

Fig. 8. Urban cockroaches in Australia: a, the American cockroach, *Periplaneta americana*; b, pronotum of the Australian cockroach, *P. australasiae*; c–f, egg cases (oothecae) of (c) German cockroach, *Blatella germanica*, (d), Oriental cockroach, *Blatta orientalis* (raised areas circular), (e) *P. americana* (raised areas elongate, 8–9).

potential health hazards because they feed both on infective substrates (such as human or animal faeces) and human food. Roth and Willis (1967) suggested that the importance of cockroaches has tended to be less appreciated than that of flies because their nocturnal activity renders them less conspicuous. Both groups carry many pathogens but evidence for disease transmission is relatively circumstantial, unlike the close causative relationships documented for many flies and other insects noted below. Very heavy infestations of domestic cockroaches can occur and their role as mechanical vectors of disease is potentially important (see Cornwell, 1968). However, they attract more attention merely as undesirable aesthetic pests (p. 33). Incidently, confusion over the place of origin of some exotic species in Australia is shown well by the names of some of these cockroaches. The American cockroach, *Periplaneta americana*, almost certainly originates from tropical Africa, and the Australian cockroach, *P. australasiae*, is likely to be native to Asia!

Bedbugs (Cimicidae: *Cimex lectularius*) can be highly debilitating to people through their bites. However, they are generally believed to have little importance as disease vectors, although Kettle (1984) noted that (in Africa) the Hepatitis B virus had been recovered from bedbugs, so their importance might need further investigation.

Both major groups of parasitic **lice**, the Anoplura (sucking lice) and Mallophaga (biting lice), are important disease vectors, with the former being the more significant. As with other ectoparasites, the effect of lice is a function of their density, so that the degree of irritation, scratching, damage to skin and possible yield losses in domestic animals are all associated with high louse numbers and, therefore, with poor hygiene conditions.

The two forms of *Pediculus humanus* (Fig. 9a) are sometimes regarded as separate species. These, commonly referred to as head lice and body lice, remain distinct in nature but can be crossed to produce intermediate forms in the laboratory. They cause irritation, but scratching in response can lead to a secondary infection and skin lesions. *Pediculus* is the vector of typhus, absent from Australia since the early days of European settlement, and relapsing fever (not in Australia). The human crab louse, *Phthirus pubis* (Fig. 9b), does not transmit any pathogenic organisms.

Other insects of veterinary importance. Other sucking lice, *Haematopinus* spp., are important pests of cattle (*H. eurysternus*), pigs (*H. suis*) and horses (*H. asini*). *Haematopinus tuberculatus* occurs on buffalo but has been found on cattle and camels in Australia and apparently causes little harm. The other three species can cause anaemia

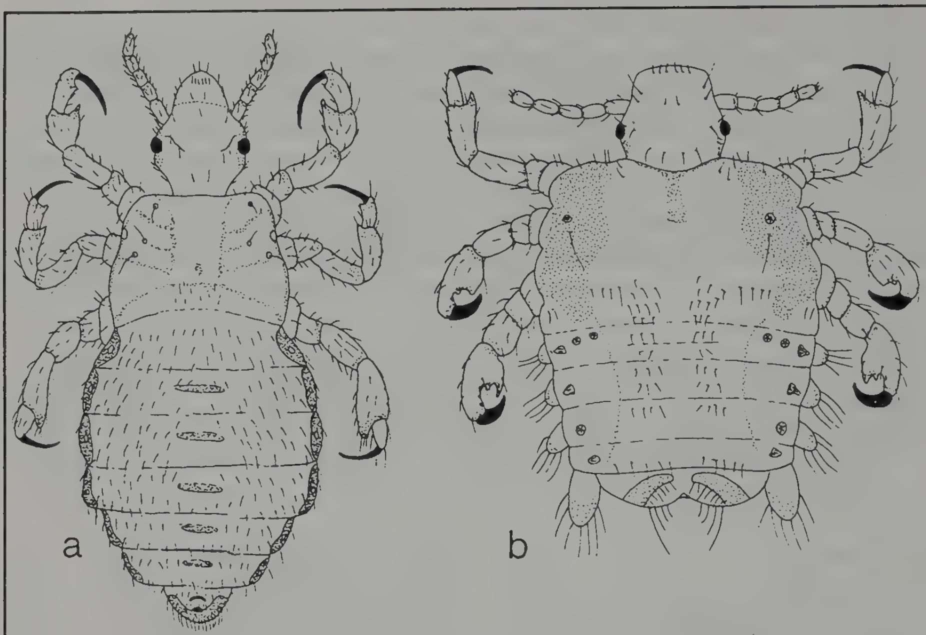

Fig. 9. The two species of human lice, Phthiraptera. a, *Pediculus humanus*; b, *Phthirus pubis*.

and general loss of condition. *Haematopinus suis* is the largest anopluran on domestic animals and can be associated with reduced growth rate of hosts. *Linognathus* spp. occur on sheep (*L. pedalis*: foot louse; *L. ovillus*: face louse) and on cattle (*L. vituli*). Moderate numbers appear to cause little harm.

In the Mallophaga, the amblycerans *Menopon gallinae* (the shaft louse) and *Menacanthus stramineus* (chicken body louse) are both important pests of poultry. The latter is the more important and large numbers cause skin irritations. Various ischnocerans occur on chickens, cats or dogs, but only *Trichodectes canis* is of veterinary importance because it can be a vector of *Dipylidium* tapeworm in dogs. The sheep louse *Damalinia ovis* is an important livestock pest.

Fleas are also of veterinary importance. Both *Ceratophyllus gallinae* and *Echidnophaga gallinacea* can be important poultry pests, for example. The latter, a 'sticktight flea', attaches to the heads of chickens and large numbers result in anaemia. In young birds, death can result and hens may suffer lowered egg production. Dog fleas (*Ctenocephalides canis*) and cat fleas (*C. felis*) (Fig. 10) can act as intermediate hosts for the tapeworm *Dipylidium caninum*.

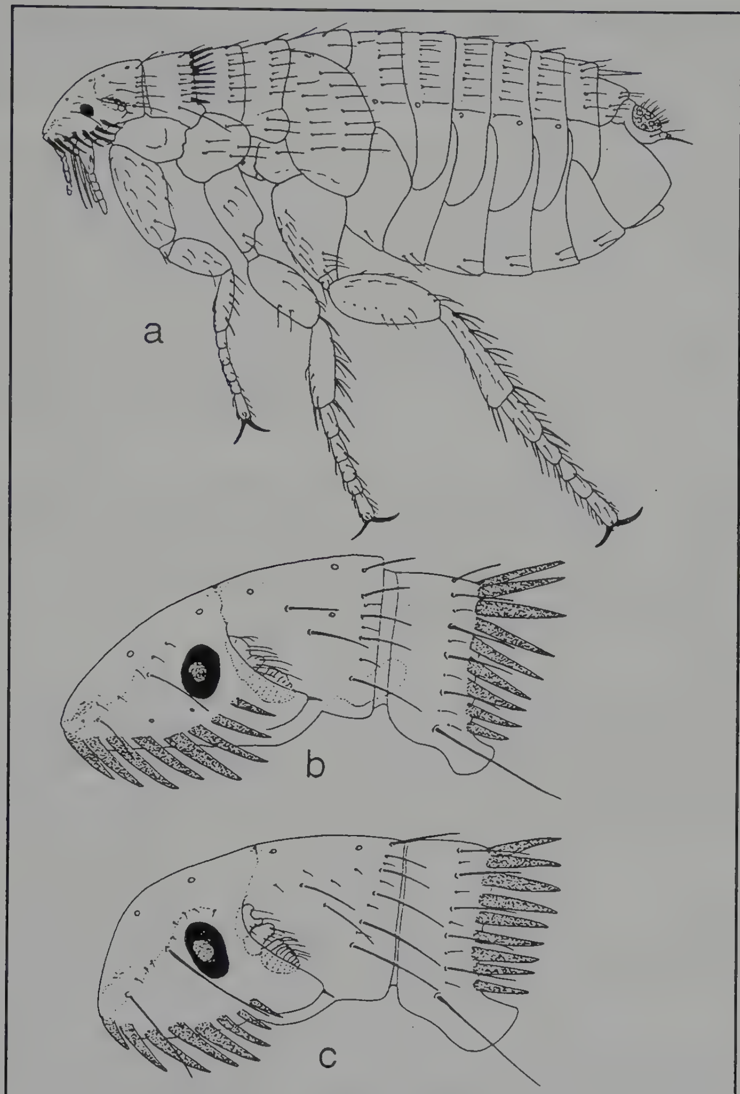

Fig. 10. Fleas of domestic pets: a, *Ctenocephalides felis*, the cat flea; b, same, enlarged anterior end; c, *C. canis*, the dog flea, enlarged anterior end.

Control. Control of most livestock pests is achieved by chemical means and by increasing the levels of hygiene. Urban cockroaches, for example, may merit a diverse control strategy (Fig. 11), incorporating trapping (using food baits), some pesticide use of household 'surface sprays' or similar insecticides, hygiene (including improved storage facilities of foodstuffs and waste disposal), and biological control (using wasps which parasitise eggs, *Tetrastichus*, or oothecae, *Evania*). There is

some likelihood of controlling lice by use of the bacterial-based insecticide *Bacillus thuringiensis*, used more commonly against phytophagous insects (especially Lepidoptera) on crops but now also under investigation against dipterous pests of livestock.

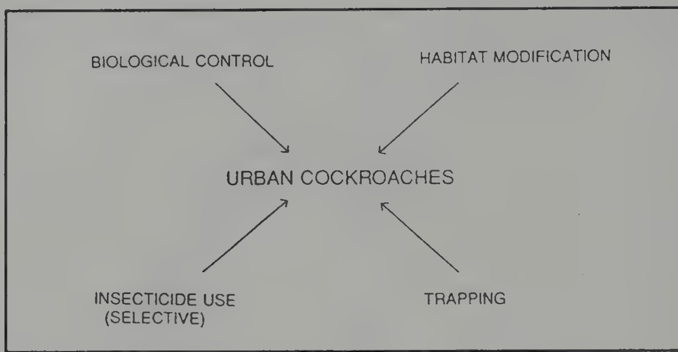

Fig. 11. Components of a control strategy for urban cockroaches. After Piper and Frankie (1978).

Buffalo fly, like the bushfly (p. 58), can be controlled by destruction of the dung breeding habitats (p. 56). Its incidence as an important pest increased after the increased use of zebu-type cattle in northern Australia led to reduced chemical use against cattle ticks. Several species of predatory beetles from southern Africa, predominantly staphylinid beetles, have been evaluated for their possible use as biological control agents against early stages of *Haematobia* in dung pads. Efforts to control this major pest are emphasising such ecologically based methods, with the aim of minimising chemical usage. Buffalo fly traps are also being designed: one recent trap, now commercially available, is used as cattle walk through (for example to or from milking sheds or water points) and brushes flies from the animals. They are retained in the trap where they die from desiccation or starvation. Daily trapping can maintain animals almost completely fly free.

Domestic pests of commodities

The medical importance of some of the exotic or cosmopolitan insects noted above is clearly rather slight, infrequent or tenuous. They integrate almost imperceptibly with a wide range of other domestic pests which have no demonstrated medical or veterinary importance but which may cause alarm or very substantial damage to stored foods and fibres. Some (such as silverfish and some cockroaches) are regarded as an affront to hygiene-conscious people, as noted in Chapter 2, but cause no real damage other

than occasional minor aesthetic damage or faecal contamination. Some ectoparasites of pests, poultry or stock, likewise, have no medical importance and are rarely if ever disease vectors.

However, many other medically innocuous insects attack stored foods or other commodities and demand massive attempts to control them. Many are transported easily by trade and thrive in stores and warehouses in many parts of the world. In Australia, many such species are naturalised. They arrived early in European settlement, have become permanently established, are widespread in the country, and some have very high economic importance. The problems they provide are exemplified well by grain- and flour-infesting beetles, which have direct impact on important export industries in Australian agriculture.

Insects have probably infested stored grains and other foods in many parts of the world since prehistorical times: flour beetles have been found in grain from Egyptian tombs of around 3,000 BC (Solomon, 1965). Such beetles are likely to have been brought to Australia in provisions with the first fleet and been here ever since—undoubtedly with frequent reinforcement from numerous more recent introductions. They are among the most important categories of pest in Australia and the need to ensure that export grain is pest-free has required substantial attention to, and investment in, their control. Most of the species involved are regarded as cosmopolitan, or nearly so, and rather few are of major or consistent economic importance, although about 200 species of beetles are associated with stored products of one form or another.

Beetles can build up to enormous populations at times. Longstaff (1986) summarised some symptoms of an early serious plague of the rice weevil, *Sitophilus oryzae* (Fig. 12), in south-eastern Australia, which was described in great detail by Winterbottom (1922). One site at Wallaroo, South Australia, contained more than 4.5 million bags of wheat. Weevils leaving the bags each day reached depths of 10–12 cm in walkways, and people reported hearing the insects moving in the sacks. Up to a tonne of weevils were collected and destroyed each day and daily losses were estimated at 40 tonnes of wheat. The Australian campaign against *S. oryzae* at that time was described as 'the greatest battle man has had to fight against stored grain pests anywhere and at any time' (Ratcliffe *et al.*, 1940; Longstaff 1986).

In general, there are two ecological categories of beetle which attack stored grain or grain products. The rice weevil, its close relative the grain weevil (*Sitophilus granarius*), and the lesser grain borer (*Rhyzopertha dominica*), attack whole grains and are thus primary pests. In contrast, flour beetles (*Tribolium* spp.: mainly *T. castaneum* (Fig. 13) and

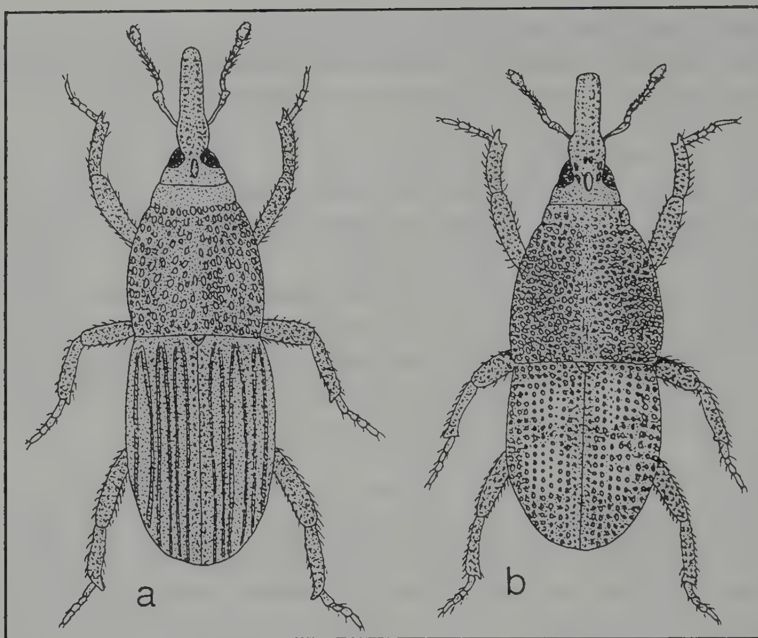

Fig. 12. Two weevils which infest stored products: a, the grain weevil, *Sitophilus granarius*; b, the rice weevil, *S. oryzae*.

T. confusum) infest broken grain, meal and flour. They are secondary pests which commonly follow the attack by primary pests. However, bag or bulk storage of grain usually provides sufficient broken cereals for them to occur early on. Other flour beetles occur, but most are generally of only minor importance, and many other beetles infest other stored products such as dried fruit or animal products.

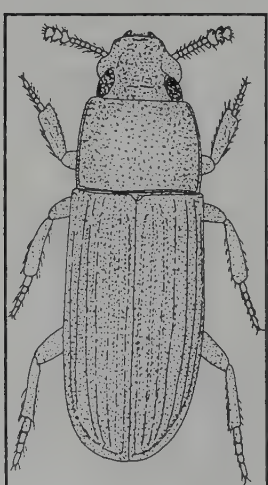

Fig. 13. A flour beetle, *Tribolium castaneum*.

Control of pests in stored products poses problems which are rather different from many other contexts. There must be no residual chemicals left on commodities destined for human foods, and the density and large bulk of grains or flour renders many control techniques technologically difficult to use. Grain was formerly stored in bags rather than in bulk and, in the case of the rice weevil plague noted above (and others), infestation started in the outermost bags of a stack. Only rarely did major infestations occur in the centre of stacks and when they did they were most commonly initiated by so-called king bags (Ratcliffe *et al.*, 1940) already containing weevils. That major plague was aggravated by a plague of mice in 1917, which caused collapse of the stacks, followed by a wet winter.

The components of a control programme for grain beetles include: (1), checking existing infestations; (2), maintaining the grain in condition suitable for export; and (3), preventing new infestations from arising. Chemical methods, including fumigation and carbon dioxide gassing to asphyxiate the beetles, and physical factors, such as the effects of temperature, moisture content and atmospheric humidity, were being studied actively by about 1940. Early attempts at fumigation (with cyanide or carbon bisulphide) were generally unsatisfactory, but substantial mortality could be achieved by 'self-gassing'; the grain was enclosed and this allowed carbon dioxide produced from the beetles' metabolism to build up to concentrations of 10 per cent or more. Following this treatment, infested wheat was sieved to remove beetle corpses and heat sterilised to kill off remaining early stages. New storage facilities were gradually constructed to be more pest-proof, especially to exclude mice, and fumigants such as methyl bromide and phosphine were then employed effectively.

However, dependence on any form of insecticide control was hampered by three substantial problems: (1), resistance of insects; (2), the need to store grains for long periods, conditions under which pest attack can increase substantially; and (3), the pressures from buyers to have grain both free of chemical residues and living and dead insects. Such grain attracts a premium from importers which was estimated at $20/tonne in 1988 (Ralph, 1988).

Use of malathion as an insecticide in grain commenced in Australia in 1960 and, as Longstaff (1986) emphasised, this chemical was a landmark in grain protection in Australia. It was used also as a prophylactic so that the whole grain harvest was treated, protecting the grain for about nine months, and helped to meet the nil tolerance standard insisted upon by some overseas customers. Resistant strains of beetles appeared by the late 1960s, and malathion had to be phased out progressively (Champ and Campbell-Brown, 1970). Development of resistance to other chemicals

gradually became widespread, prompting the urgent need to investigate other strategies of control from the early 1970s onward. Insects can develop resistance to a given pesticide very rapidly, and the potential for developing new chemicals for use in grain silos is economically limited, especially as any such chemical must meet the requirements of (1) a broad range of activity so that it is effective against all beetle pests present, (2) degradation within a predictable time and to zero/near zero levels, and (3) low or zero toxicity to mammals.

Much recent emphasis has been placed on use of phosphine fumigation, for which the need is to employ a low dosage over a substantial period so that tolerant growth stages of the beetles can progress to more susceptible ones. For this to be effective, adequately gas-tight silos are needed. This can be expensive to achieve. A technique (SIROFLOW®) involving a constant low concentration phosphine flow is now used extensively both to eradicate any insects in the grain when it is stored and to protect it from new invaders, and entirely tight silos are not needed for this to be effective. This method is also much cheaper than other chemical protection. Physical methods of control, such as heating and the use of controlled atmospheres (particularly with high carbon dioxide) have also been investigated extensively in recent years.

Stored products pest control is unusual, also, in that the methods are employed in very specific sites, and generally have few or no ramifications or spill-over into other environments. Biological control is of minimal importance and unlikely to increase in use in Australia in this context. Such precisely directed control, however desirable, is often much more difficult for pests outside silos.

Ecological diversity of beetle pests of stored products is reflected in the range of commodities attacked. In addition to grains and flour, particular beetles attack other seeds (some Bruchidae may initiate attack in the field and be transported into storage: p. 73), nuts, dried fruits, bacon and animal hides. Many such associations are of long standing. Timber-in-service pests are noted in the next chapter. The range of beetle pest contexts is paralleled by that of Lepidoptera: moths such as the house moths and warehouse moths (Oecophoridae), grain moths (Gelechiidae) and clothes moths (Tineidae) are the most important groups containing commodity pests, and a few representatives of other families are also represented.

The case-bearing clothes moths, Tineidae, can exploit a great variety of natural or manufactured keratin-based goods, including wool, feathers, fur, leather and silk, and seven widespread species are pests in Australia (Robinson and Nielsen, 1987). Some of these occur only infrequently and

some species identifications have probably been confused in the past; Robinson and Nielsen noted that there are very few records of true *Tinea peleonella*, for example. Because of their different patterns of insecticide resistance (Robinson and Nielsen, 1987), correct identification of these moths has considerable practical importance.

Other pests of people

A few exotic insects in Australia are perceived as dangerous because they can cause direct harm to people by being aggressive and stinging or biting, and often occur in large numbers. Honeybees have benefits to offset this and in urban areas the most significant insects in this category are other social insects, namely, two species of social wasps, the European wasp (*Vespula germanica*) and the English or common wasp (*V. vulgaris*) (Fig. 14). The latter occurs in Victoria, but *V. germanica* is widespread. It has increased rapidly in distribution over the last decade or so and occurs throughout Tasmania, in central coastal New South Wales and the metropolitan areas of Adelaide and Fremantle. Earlier known from New Zealand (Thomas, 1960), *V. germanica* was first recorded in Tasmania in 1959 (Spradbery, 1973b) and from Western Australia in 1977 (Crosland, 1991). The first incidences noted from New South Wales were of queen wasps intercepted by quarantine authorities, one on *Pinus radiata* timber (1954) and one on tree tomatoes (tamarillos, 1968) from New Zealand (Smithers and Holloway, 1977). There seems little doubt that such accidental transport of (?hibernating) queens could have been the mode of arrival of both species. *Vespula germanica* is now extending into Queensland and progressively outward from southern urban centres. Spread to some towns in Victoria is likely to reflect human transport. The first nests in some towns were discovered in the homes of people who had moved recently from Melbourne (Crosland, 1991). Climatic tolerances of *V. germanica* imply that it could extend as far north as Cairns (Spradbery, 1988) and that it can potentially colonise most of the eastern seaboard north to around Rockhampton (Spradbery and Maywald, 1992) Prospects for containing or controlling the wasp appear to be small. Young queens may disperse naturally and have founded colonies up to about a kilometre from their parental nest. *Vespula germanica* is a Palaearctic species and *V. vulgaris* is naturally Holarctic.

Both in Australia and New Zealand the wasps are commonly perennial rather than having colonies which die off each winter to be re-established from hibernating queens in spring, as is usual in the northern hemisphere. This change can result in very large colonies: as examples, Spradbery (1973b) noted nests with more than a million cells in Tasmania, and Thomas (1960) recorded a nest weighing about 45 kg in New Zealand.

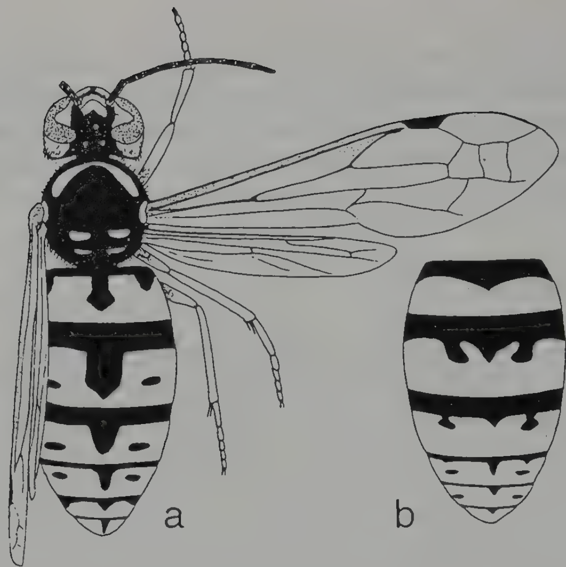

Fig. 14. Introduced social wasps: a, the European wasp, *Vespula germanica*; b, different abdominal pattern of the English wasp, *V. vulgaris*.

The superabundant wasps present severe problems in urban and surrounding areas. These range from direct stinging (the threat of being stung is a primary concern to many people, and can be aggravated by the wasps' aggressive response if they are swatted at) to interference with recreational or commercial activities. Wasps may become common in recreational areas, such as picnic grounds, parks or playing fields, in which they are attracted to human foods or sugary or fermenting drinks. They can also result in reduced attendance at holiday resorts, golf courses, open air cafeterias and the like. Their predilection for ripe fruit has led to the wasps being a nuisance to fruit pickers and, in New Zealand, there are cases of the work schedules of road construction teams and forestry workers being changed because of wasps (Perrott, 1975). *Vespula germanica* is also seen as a cause of financial detriment to beekeepers because they rob hives or cause direct loss to bees (Thomas, 1960, New Zealand). Losses to beekeepers in Tasmania were recently estimated at $15,000/year (Crosland, 1990).

The wasps also nest in or under houses and so may impinge directly on individual householders. Such occurrences result in many requests to local councils for nest destruction or removal. Although the wasps are thus primarily urban/suburban pests, there are concerns over their spread into more natural environments and interactions with native biota (Chapter 6). Because they have been present there for longer, this spread (and the interactions between the two wasp species) has been documented more

fully in New Zealand, where replacement of *V. germanica* by *V. vulgaris* in some areas has been used as a case history of species replacement (Harris *et al.*, 1991). *Vespula germanica* reached New Zealand in the 1940s and became established throughout the country but *V. vulgaris* invaded only in the late 1970s. It then spread rapidly and now occurs in some habitats occupied previously by *V. germanica*. It has replaced the latter in some places. Generally (in New Zealand), *V. germanica* is the more abundant species in non-forested rural areas, and *V. vulgaris* the more numerous in *Nothofagus* forests. In forests, *V. vulgaris* forages mainly on shrubs and saplings and *V. germanica* among forest litter, so that different foraging patterns might facilitate coexistence (Sandlant and Moller, 1989; Thomas *et al.*, 1990, Harris *et al.*, 1991). Some of the ramifications of this extension into rural environments are noted in Chapter 6.

Two methods of control of these vespid wasps are used in Australia. Direct poisoning of individual nests is used for short term local control of specific colonies and can be especially effective early in infestations. If these are not found, rapid spread of wasps can ensue. More than 23,000 nests were destroyed in the Melbourne metropolitan area in 1989, for example, and the costs of nest destruction in that year were estimated at more than $600,000 (Crosland, 1991). Poisoned baits have not been employed extensively in Australia, although Harris (1978) cited several examples in North America against urban wasps (including *V. vulgaris* in California) where foods such as cooked horsemeat or fish-flavoured cat food combined with insecticides led to substantial decrease in numbers of foraging wasps. A European ichneumonid wasp, *Sphecophaga vesparum*, a parasitoid which has been screened to ensure its host-specificity, has been released in Victoria (following earlier release and study in New Zealand). The first Victorian releases were made at three sites near Melbourne in late 1989. Soon after that, the (then) Department of Conservation and Environment sought support from 40 local municipalities which were asked to contribute $3,000 each to expedite the parasitoid rearing and release program. Each contributor would have at least a thousand *Sphecophaga* released in the area. Many municipalities contributed and the program is continuing. It is still too early to determine whether or not it is achieving the desired result.

Very high levels of destruction of queen wasps may have little effect on subsequent populations. An early attempt to destroy hibernating queens of *V. germanica* in New Zealand by offering a bounty of 3d/wasp resulted in claims for 118,000 wasps in three months (Thomas, 1960) with negligible effects on populations. Indeed, Spradbery (1973a) suggested that culling of winter queens might even increase the number of wasp nests the following season by reducing competition for suitable nest sites.

The Argentine ant, *Iridomyrmex humilis*, is an important and aggressive pest in urban areas and is spread easily by transport from nurseries and stables, for example. In Western Australia, an Argentine Ant Control Committee was set up in 1954, when the species was already well established in Perth and Albany. Chemical control methods have been used continually, and by 1971 heptachlor had replaced dieldrin as the primary insecticide. Applications on a 3 x 3 m grid pattern led to eradication of colonies. By May 1986, some 30,750 ha of infested ground had been sprayed, with more projected for treatment in the State.

In urban regions, *I. humilis* is regarded primarily as a domestic pest. It commonly nests near homes in habitats such as crevices in the ground or pavement, or under plantpots, and enters houses seeking sugar. The amount of damage they cause to foods is usually insignificant but, like other ants in houses, Argentine ants can cause annoyance and occasional aesthetic damage.

Dung beetles

The biological control of dung is one of the most unusual and important stories involving exotic insects in Australia, and one which added greatly to understanding of the subtle ecological relationships which can exist between insects and their food resources. Persistence of dung produced by cattle and other exotic hoofed stock led to serious problems of pasture pollution, manifested by growth of inedible grasses and increased breeding habitats for pests such as the introduced buffalo fly and, particularly, the native bush fly.

The problems arose because this dung was not being broken down to any significant extent by native Australian dung beetles (Scarabaeidae). These beetles had evolved in association with the drier pellet-like droppings of native marsupials and could not utilise the large moist masses produced by cattle. A few native dung beetles can indeed use cattle dung, but these tend to occur only sporadically and not to be capable of major or widespread impact.

In the early 1960s, a major effort was begun by CSIRO to remedy this situation. This involved introducing dung beetles from countries with native mammals which produce dung of the form giving problems in Australia. Between 1968 (when the first successful releases were made) and 1982, more than 45 species were imported from Africa, Europe or Asia. Many of these were released after quarantine study and clarification of their life histories and basic biology. The range of species selected for release included those suited to a wide range of different climatic regimes parallel to those in Australia. The species which have become established are listed in Table 4 (after Tyndale-Biscoe, 1990).

Table 4. Exotic dung beetles introduced and established in Australia. +, introduced or established. Data from Tyndale-Biscoe (1990).

Species	Origin	Introduced/Established in : NSW	WA	Q	NT	SA	V	T
Onitis alexis	Africa, Europe	+/+	+/+	+/+	+/+	—	—	—
O. aygulus	S. Africa	+/+	+/+	—	—	+/+	—	—
O. pecuarius	S. Africa	+/+	—	+/+	—	—	—	—
O. caffer	S. Africa	+/+	+/+	+/–	—	—	—	—
O. viridulus	Africa	+/+	—	+/+	+/+	—	—	—
Euoniticellus intermedius	Africa	+/+	+/+	+/+	+/+	+/–	+/-	—
E. africanus	Africa	+/+	+/–	+/–	—	+/–	+/+	+/–
E. fulvus	Europe, N. Africa	+/+	+/+	—	—	+/+	+/+	+/+
E. pallipes	Europe, Asia	+/+	+/+	—	—	+/–	—	—
Liatongus militaris	Africa	+/+	+/–	+/+	+/+	—	—	—
Onthophagus taurus	Europe, Asia	+/+	+/+	—	—	+/+	+/+	+/+
O. binodis	S. Africa	+/+	+/+	+/–	—	+/+	+/+	+/+
O. gazella	Africa	+/+	+/+	+/+	+/+	+/–	+/–	+/–
O. nigriventris	E. Africa	+/+	—	+/+	—	—	+/-	—
Sisyphus spinipes	Africa	+/+	—	+/+	+/–	—	—	—
Geotrupes spiniger	Europe, Asia	+/+	—	—	—	—	—	+/+
Hister nomas[1]	S. Africa	+/+	+/–	+/+	—	—	+/–	+/–
Total species		17/17	12/9	12/9	6/5	8/4	8/4	7/4

[1]See text.

The beetles were imported as surface-sterilised eggs, which were then inserted into artificially prepared dung balls. Emerging adults of that generation were in turn given dung in which to lay, and eggs of this generation were also surface-sterilised and reared. Only after that second generation in quarantine were the beetles mass-reared in insectaries.

Field studies in South Africa and elsewhere to select candidate species from the many potential ones which could be imported led to many being rejected because they had low reproductive levels, or bred slowly or not at all in captivity.

Some species, such as *Onthophagus gazella* in northern Queensland, increased in numbers spectacularly after introduction and the rapid degradation of dung observed produced very favourable responses from farmers. Studies on this species by Bornemissza (1970) showed that a density of four beetles per 100 cc of dung resulted in entire dung pads being broken up and buried within 30–40 hours, so that an 80–100 per cent reduction in emerging bush fly numbers ensued. Complete burial of the pad within 24 hours gave complete control of flies, and few or no bush flies emerged if even half the pad was buried over that period. By about 1975, control of bush fly by *Euoniticellus intermedius* was evident in New

South Wales, and this beetle also spread and increased rapidly in numbers. Other species also increased during the 1970s, to the levels of 1,000–1,500 individuals/pad (*O. gazella*) or up to 3,000 beetles/pad for smaller species.

Spread of the more common established species through climatically suitable areas is achieved largely by collecting adult beetles attracted to dung in the field, and releasing them elsewhere. Tens or hundreds of thousands of beetles can be moved in this way and farmers have been encouraged to disperse beetles actively (Houston *et al.*, 1982). Such collections seem to have no noticeable effect on the parent population (Tyndale-Biscoe, 1990). Release is made by putting the beetles on fresh dung pads in paddocks stocked with cattle or horses. Several hundred beetles of a species should be liberated in the same place and up to three to five years may be needed for beetle numbers to build up to effective levels.

The mosaic of beetle species introductions involved close appraisal of climatic preferences of each in order to predict likely areas of establishment and their capability to reduce dung throughout the year. Examples of the resulting maps (Figs 23–25: p. 81) are a useful guide to where particular species could survive in south-eastern Australia. Some have rather limited potential, whereas others could apparently survive over much of the region. The greatest number of exotic dung beetles may be expected to succeed in eastern New South Wales and southern Queensland. In contrast, only about three species may be expected to become widespread in the Northern Territory.

The effects of introduced dung beetles against bush fly have been augmented by introducing a parasitoid wasp from New Zealand, initially into New South Wales, and the southern African beetle *Hister nomas*. This species lives in dung, and both larvae and adults are predators on fly larvae and other small dung denizens. This comprehensive biological control programme is unusual in attacking both a foodstuff of a pest (dung) and the pest itself, using different biological agents.

Chapter 5

Exotic Insects on Plants

The most frequent feeding habit of insects is eating plants. Virtually any kind or part of a plant is attacked by some kind of insect, and the literature on insects which feed on crops is voluminous. Particular insects can be categorised by their feeding method as, for example, foliage-chewers, sap-suckers, stem-borers, foliage-miners, gallers and so on, and different insects feeding on the same plant may occupy these and other roles. They can thereby cause vast economic losses, either through direct reduction in yield, or by producing blemishes which reduce market value. Apples blemished by caterpillars or citrus scarred by scale insects are not acceptable as prime individual fruit for supermarkets and may need to be processed for juice at a fraction of the price they would otherwise command. Many sap-sucking insects, such as aphids (p. 66), have an additional pest-role, because they can transmit plant viruses between plants. In short, insects are human beings' main competitors for vegetable resources.

The same feeding habit can sometimes be turned to human advantage by using plant-feeding insects as agents to control weeds. Many exotic insects in Australia are pests of plants (mainly also exotic) and others have been imported to control exotic weeds. Some examples of each are outlined below to indicate the many situations in which they are of major concern.

Pests of forestry crops

Introduced softwood trees, predominantly of radiata or Monterey pine, *Pinus radiata*, exemplify an important forestry crop susceptible to extensive damage from exotic insects introduced from the northern hemisphere. Two of these pests have caused particular concern. A woodwasp, *Sirex noctilio* (Fig. 15), has been the target of the most extensive control campaign mounted in Australia against an exotic forestry pest; and a bark beetle, *Ips grandicollis,* has also attracted much attention, initially in South Australia (Morgan 1967). Depredations by both species continue.

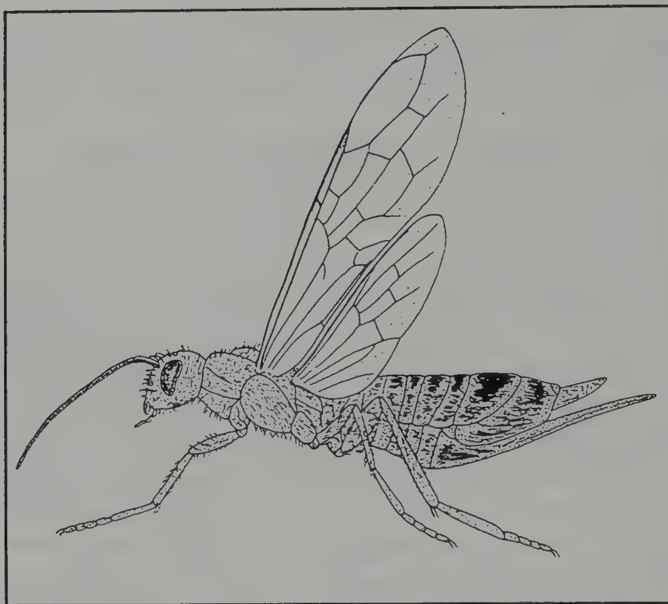

Fig. 15. The Sirex woodwasp, *Sirex noctilio*.

Sirex woodwasp. Although it was present in New Zealand from around the turn of the century, *Sirex* was not known from Australia until March 1952, when it was discovered in a pine plantation near Hobart airport, Tasmania. It is unusual among woodwasps in that it can kill living trees, and mortality of trees in that plantation (at Pittwater) reached about 40 per cent by 1959 (Taylor, 1981). The woodwasp was found in Victoria in 1961, and fears that it would spread to the large areas of pine plantations in that State and South Australia led to the setting up of a 'National Sirex Fund' and thence of a large research programme on the biology of the insect and its relationships with its host trees and natural enemies. Many State organisations become involved and CSIRO commenced studies on biological control in 1962. Searches for parasitoids were made in many European countries. Several species of the wasp groups Ichneumonidae, Cynipoidea and Stephanidae were introduced and released successfully. These parasites controlled *Sirex* to some extent but their overall effect has generally proved to be secondary to that of parasitic nematode worms. Study of these worms, *Deladenus* spp., which sterilise the female *Sirex* and cause them to lay sterile eggs—or, rather, egg-shells filled with juvenile worms, thus transferring them to another host tree—broke new ground in the control of insect pests. Their systematics and biology were clarified by Bedding (1968, 1972, 1979; Bedding and Akhurst, 1974, 1978), and it was possible to rear the worms in enormous numbers in the laboratory. The techniques have since been modified for

mass production of nematodes infesting other insect pests. Nematodes, different strains of *Deladenus siricidicola*, were liberated in the Pittwater plantation in 1972–73, and more than 90 per cent of *Sirex* emerging from infested trees were parasitised by about 1975. Hundreds of millions of nematodes were released throughout the range of *Sirex* in Tasmania and Victoria during the mid 1970s.

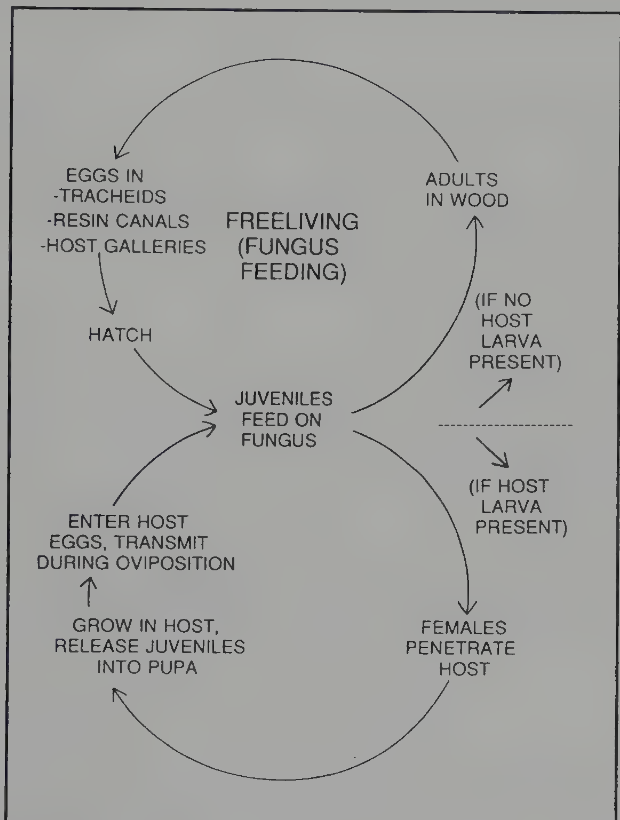

Fig. 16. Life cycle of *Deladenus* nematodes, parasites of *Sirex*. After Taylor (1981).

The life cycle of *Deladenus* (Fig. 16) has two phases, one in the tree, and one in the wasp. The free-living worms feed on fungus (*Amylostereum*) symbiotic with *Sirex* and which is both spread by the female *Sirex* and used as food by the woodwasp larvae. Large populations of fungus-feeding nematodes can build up in a fungus-infected tree. If the nematode juveniles occur near healthy *Sirex* larvae, they mature into infective females which, after mating, penetrate the larvae to commence a parasitic phase. A hundred or more infective females can invade a single *Sirex* larva. They

release juvenile worms into the host's body cavity whilst it is a pupa. These migrate to the reproductive system and the female *Sirex* is then sterilised, though males remain fertile. However, parasitised female *Sirex* oviposit normally, introducing both the symbiotic fungus and worm-filled eggs into a pine tree. The worms then move into the tree, resume the fungus-feeding stage, and the cycle is completed. Nematodes are introduced into the plantations by inoculating them (with fungus) into pine trees; they can then be spread rapidly by *Sirex*, at the same time markedly reducing *Sirex* population levels and, thence, tree mortality.

Nematodes and parasitoids generally led to containment and reduction of *Sirex* infestations. Outbreaks can still occur: one devastating one eventuated in the so-called green triangle—the area bordering southern South Australia and Victoria—in April 1987, and the knowledge obtained from the earlier programme facilitated rapid and effective response to this (Haugen, 1990).

Bark beetles. *Ips grandicollis* is the most important of a number of introduced bark beetle pests (Neumann, 1987). It was reported from South Australia in 1943 and from Western Australia in 1952 (Morgan, 1967). These probably represented two separate introductions, possibly associated with different importations of pine timber with bark. It was found also in bark on packing crates in South Australia. *Ips* can cause mortality of trees and also contribute to blue-staining of pine sapwood by introducing fungi. It can build up in numbers rapidly and undergoes up to five generations each year. The beetles can attack healthy trees as well as stressed or recently dead ones. They cause additional harm to the former categories by facilitating entry of fungus leading to wood decay.

Neumann (1987) suggested that *Ips* had been mainly a secondary pest in Australia, not contributing substantially to tree mortality. In South Australia mortality had been low over about 40 years, and in Western Australia, sporadic outbreaks through the 1970s resulted in some deaths but these were usually of drought-stressed trees. Healthy trees have also suffered little mortality in Victoria, Queensland (*Ips* became established in both States in 1982), or New South Wales (1983). Of major concern in New South Wales, particularly, is the potential for major fungus-staining of timber (Stone 1990). The species' introduction to Queensland was apparently in a single consignment of veneer logs from South Australia (Wylie and Peters, 1987). Neumann (1987) believed that it would colonise most commercial pine areas in Australia within a few years.

A diverse control program is being pursued against *Ips* in Australia. It includes silvicultural controls, biological control, and the use of pheromones.

Silvicultural controls (recommended by Neumann and Morey (1984) in Victoria) include:

(1) chopping or macerating log residues, or burning of slash growth from forestry operations;

(2) rapid salvaging of high quality trees damaged (e.g. by fire or lightning strikes) and burning residual slash;

(3) restrictions on clear-felling periods for compartments near older thinned stands, and in which beetle numbers can be high; and

(4) rapid transport of logs (within two days of felling) if the mill is outside the *Ips* area at particular times of the year (October to May).

Biological control efforts have been supported strongly, and several insect predators and parasitoids have been introduced. One parasitoid (the torymid wasp *Roptrocerus xylophagorum*) has established and dispersed considerably. The effects of these natural enemies have not yet become clear.

With regard to pheromones, a synthetic commercial preparation of bark beetle pheromone has been tested in Victoria, with very promising results (Neumann, 1987), and large populations of beetles can be trapped. The traps are also valuable in detecting or surveying beetles because they are sensitive to very small populations.

Another bark beetle has attracted considerable attention in Australia because, although it is not itself regarded as a damaging pest, it has the potential to act as vector for a disease of ornamental trees: the fungus causing the disease is not yet present in Australia, and studies of the elm bark beetle, *Scolytus multistriatus,* have been designed in part as pre-emptive, should control ever be needed (Neumann and Minko, 1985). The disease, Dutch elm disease, has killed vast numbers of elms in the northern hemisphere, and is caused by a fungus, *Ceratocystis ulmi*, closely related to that transmitted in pines by *Ips*. Elms are valued ornamental and shade trees in Australia's southern capital cities. The beetle was discovered in January 1974 near Melbourne. By 1975 it was discovered nearly 100 km further west, at Ballarat and Castlemaine, where it may well have been present before that time (French *et al.*, 1977). Pheromone bait traps were developed to monitor the spread of the beetle in Victoria, and by 1984 it had become widespread (Neumann and Minko, 1985). If the fungus disease reaches Australia, early detection is likely to prove important in instituting beetle control measures accompanied by sanitation, viz. the rapid removal and destruction of infected trees.

The exotic bark beetles established in Australia are listed in Table 5.

Table 5. Exotic bark beetles established in Australia.

Species	Source	Host(s)	Pest status
Ips grandicollis	North America	Pines	High
Hylastes ater	Europe	Pines	Occasionally high
Hylurgus ligniperda	Europe	Pines	Occasionally high
Phloeosinus cupressi	North America	Cypress	Occasional
Scolytus multistriatus	Europe	Elms	Potentially high

A pest of ornamental trees

The elm leaf beetle, *Pyrrhalta luteola* (Fig. 17), has been ranked as 'one of the most important shade tree pests in the Palaearctic region' (Olkowski *et al.*, 1978). This chrysomelid was introduced into the United States in 1834 and became the target of biological control attempts there early this century. As with a number of other pests, the biological control expertise gained in North America became relevant to Australia when the beetle reached this country. It was first recorded in Australia on the Mornington Peninsula, Victoria, in 1989. It attacks both golden and English elms and, as with the elm bark beetle (p. 63), concern rapidly arose over its depredations on some of the world's finest ornamental stands of elms.

Adult beetles hibernate in sheltered sites and emerge in spring, when they fly to elms and lay clusters of eggs on the foliage. Heavy infestations of larvae can completely defoliate trees and, after two or three

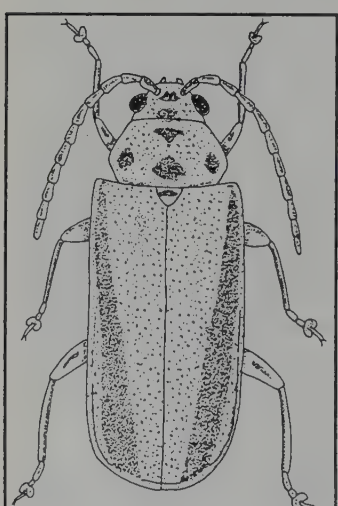

Fig. 17. The elm leaf beetle, *Pyrrhalta luteola.*

generations, the beetles again seek retreats in autumn. During winter they can be transported easily in vehicles and goods and people are asked to check cars and caravans carefully for beetles when leaving the Mornington Peninsula to help curtail the spread of the beetle from this popular holiday area to Melbourne and beyond. Likewise, elm material from infested trees should not be removed from the site.

An egg parasitoid has been introduced from California and released, but it is not yet known whether it will be effective against *Pyrrhalta*. One possible problem is that it has a different diapause regime and may not attack eggs of the late summer generation in the field. Trapping the larvae on adhesive bands as they move down the trees to pupate in ground litter is also a facet of control and population monitoring.

Pests of orchard crops

The most important of the wide range of insect pests in orchards in temperate Australia are tortricid moths. One, the light brown apple moth (*Epiphyas postvittana*), is native but two others, the codling moth (*Cydia pomonella*) and the Oriental fruit moth (*C. molesta*), are exotic. Both have been important in leading to the development of controlled mating disruption as a facet of integrated control programmes against lepidopteran pests. *Cydia pomonella* is a major pest in all States except Western Australia, and *C. molesta* is particularly widespread in south-eastern Australia. *Cydia pomonella* is a pest on apples (especially on late varieties such as Granny Smith). It also infests pears and quinces as primary hosts (Bovey 1966) but a number of secondary (walnuts, stone fruits) and accidental hosts are also used. *Cydia molesta* is particularly important on peaches and nectarines. Larvae of both moths ruin fruit, reducing both crop size and quality. Surface-blemished fruits are necessarily downgraded from prime market quality, and fruits which caterpillars have entered are rejected. For codling moth, Geier (1981) noted that 50–100 per cent of fruits may be attacked in inadequately protected mainland orchards.

Codling moth is believed by Geier (1981) to have been introduced repeatedly into Australia with exotic plants, packing material and other material in which the overwintering larval cocoons could be transported easily. It was found in Tasmania in the 1850s (Froggatt, 1909), in Victoria in 1885, and in New South Wales and Queensland shortly afterwards. Absence in Western Australia is due to regulatory control and prompt reaction to a number of outbreaks there from 1903 (at Albany) to 1993.

The course of one such outbreak in Western Australia was traced by Geier (1970) as follows:

(1) infested fruit, or larvae in overwintering cocoons, evade quarantine inspection, complete development, and a female reproduces successfully with her offspring surviving to maturity and reproduction;
(2) a colony is thus established, which continues to increase and spread until detected;
(3) when detected, State authorities are notified;
(4) the affected area is searched, the point of original infestation determined and buffer zones delimited;
(5) extermination begins with infested orchards being bulldozed and burned together with packing sheds and related constructions, and trees in the buffer zone are pruned;
(6) a severe spraying program is initiated and continued for several seasons; and, finally,
(7) the emergency ends after a period of quarantine.

This operation may last for five years or so. At Nannung, from 1951–1956, for example. This sequence demonstrates the enormous 'tactical response' that an unexpected occurrence of an important pest may demand and underlines the importance of interstate quarantine measures for various infestable commodities.

Control of both species has traditionally been by spraying, with a number of spray applications each season, but the costs of this and resistance problems have necessitated explorations for other methods since the 1960s, concurrently with detailed studies of the ecology and life systems of the moths. Efforts have been made to develop strategies involving the use of their specific pheromones, both to monitor local populations to determine the optimal timing of insecticide applications, and to disrupt mating as a way of decreasing reproduction and, hence, effective population levels. The latter is more advanced for *C. molesta*, for which it has been used commercially for some years. By putting large numbers of pheromone-dispensers (recommended rates of four/tree or 1,000/hectare) in orchards twice a year, for example on hollow twist-ties from which the chemical gradually evaporates, a sufficient number of false trails can be laid to confuse the normal system by which a male moth locates a female by following her pheromone trail to its source (Davidson, 1985).

Pests of field crops

Aphids. Exotic insects constitute only a small component of the Australian fauna of most groups. Aphids are an important exception to this, as exotic species dominate the fauna. Of approximately 160 aphid species in Australia, only about 20 are endemic (mainly associated entirely

with native vegetation), another 20 or so are widespread species for which Australia constitutes part of a broader natural range, and the remainder are exotics. Many of these are pests (Maelzer, 1981).

Aphids have two components to their pest status, both related to their feeding on plant saps. First, they can cause direct injury and yield loss to the crops and, second, they can act as vectors of important plant diseases such as cereal viruses. They can thereby act as a conduit for spreading such diseases within a crop stand and further afield. The relative importance of these roles differs between species but the combined effect can be devastating and cause vast economic loss. Because of their small size and classic 'r-strategy' (p. 17) adaptations, aphids disperse easily and over great distances in aerial plankton and are also transported easily by human agency. Carver (1988) noted that many can feed on common urban plants, weeds and grasses, abundant in and around airports, and that the cut-flower trade is becoming more international, providing another likely avenue for transport of such small phytophagous insects. As they are perhaps the most important group of agricultural insect pests in temperate parts of the world, aphids have been studied in great detail. Some species have life cycles in Australia simplified in various ways from northern hemisphere populations: normal overwintering eggs may be absent in all but the coldest regions, for example. Development of high populations depends largely on climate, and short term variations in weather may determine whether pest situations develop.

Some species are documented soundly as recent arrivals in Australia. The spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata*) arrived in 1977 and the blue green aphid (*Acyrthosiphon kondoi*) only about two months later, the latter probably representing introductions by people. *Therioaphis trifolii* was found initially in Queensland in March 1977. It was discovered in Victoria and New South Wales in April, and in South Australia in May, and had spread to all mainland States within about a year (and to Tasmania in 1980). Rapid spread in South Australia was monitored closely (Fig. 18, Wilson *et al.*, 1981; Swincer, 1986). The aphid spread during the cooler months and by April 1988 occupied all areas in the State which contained susceptible host plants. *Therioaphis trifolii* was regarded as a very successful invader in south-eastern Australia and designated the most important pest of lucerne only a year after being found in South Australia. *Acyrthosiphon kondoi* spread from Queensland to Tasmania and South Australia over a similar period. Both of these species are major pests of lucerne (*Medicago sativa*) and their control nationwide was coordinated by an expert panel of the Standing Committee on Agriculture, with several strategies being investigated, namely plant-breeding for aphid resistance, chemical control, and biological control. In large numbers, *T. trifoli* affects lucerne production in two ways, directly by

causing stunting and plant mortality, and indirectly by producing excessive amounts of honeydew which clog harvesting equipment and foster growth of sooty moulds which reduce hay quality.

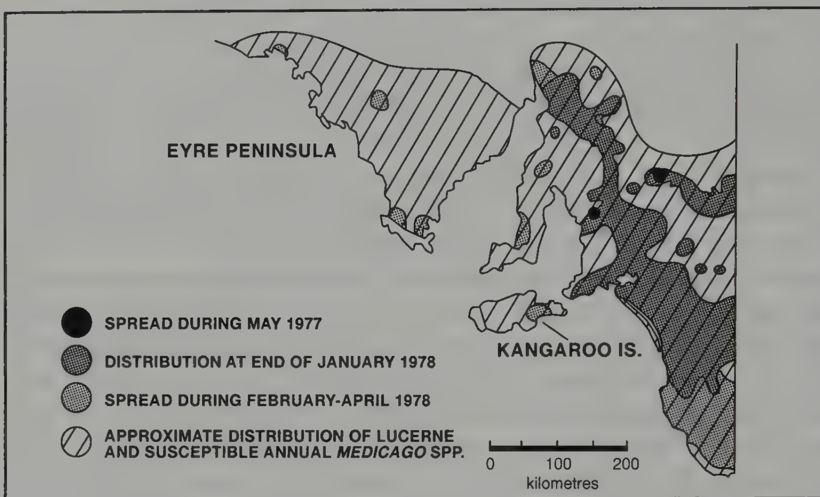

Fig. 18. Spread of the spotted alfalfa aphid, *Therioaphis trifolii maculata*, after its initial discovery in South Australia. After Wilson *et al.* (1981).

One 'advantage' with such cosmopolitan pests is that much is likely to be known already about their natural enemies and their biology, so that, for example, it was possible rapidly to import stocks of the parasitoid wasp *Trioxys complanatus* (which attacks *T. trifolii maculata*) from California. Releases of this wasp were made from August 1977 and its effects monitored for some years (Hughes *et al.*, 1987). By 1978, nearly 400,000 wasps which had been mass-reared in captivity had been released in New South Wales and Victoria and stocks sent to other States to start locally-controlled mass-rearing operations (Fig. 19). Likewise, four varieties of parasitoid of the blue green aphid were imported from various countries in late 1977 and releases of two of these (*Aphidius ervi, Ephedrus plagiator*) made from December 1977, the former in Tasmania, Victoria and New South Wales, and the latter also in Queensland and South Australia. *Trioxys complanatus* proved to be very effective after it became well established in 1979. Since then, this wasp, aphid pathogens and resistant plant varieties have kept the aphid generally below economic damage levels. However, the wasp was not effective in South Australia (Wilson *et al.*, 1982, Allen 1986), probably because of excessive heat so that it was particularly ineffective during summer and in dryland lucerne crops. Greater reliance is placed on resistant lucerne varieties in that State. *Aphidus ervi* proved effective against *A. kondoi*.

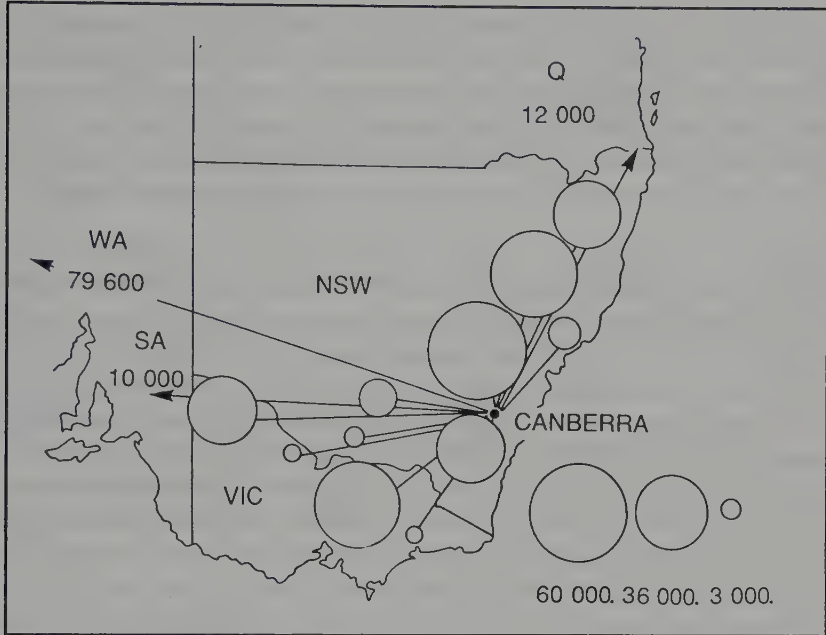

Fig. 19. Distribution and release of the aphid parasitoid wasp, *Trioxys complanatus*, in Australia. Numbers consigned between August 1977 and May 1978 are shown; consignments to Queensland and Western Australia were used to commence mass-rearing operations in those States. After CSIRO Division of Entomology, Annual Report 1977–1978, with permission.

The pea aphid, *Acyrthosiphon pisum*, was first recorded in Australia (Victoria) in January 1979 and, again, it was possible to respond rapidly to this by releasing parasitoids from stock from New Zealand and the USA. It was possible to benefit from recent similar experiences with lucerne aphid parasitoids in designing efficient mass-rearing systems for this aphid's natural enemies.

The rose grain aphid, *Metopolophium dirhodum,* is another recent arrival, having been found in June 1984 in New South Wales (Carver, 1984). *Rhopalosiphum insertum*, the apple-grass aphid, another pest of cereals, arrived in 1982 (it was attacked rapidly by *A. ervi*), and several other species were also recorded for the first time in the 1970s and early 1980s (Carver, 1988).

These are examples of recent invasions, all of which have stimulated collectively a greater need for biological control, predominantly using parasitoids and/or pathogenic fungi as the agents. In some cases, good control has been achieved. Unusually among parasitoid-insect host relationships, the wasp eggs and larvae can be dispersed in adult winged

aphids (most parasitoids of other insects occur solely in immature host stages) and Carver (1988) cited several studies where this is claimed to aid dispersal of the control agent and, thus, enhance its rapid effectiveness in the field. The importance of this strategy is, though, controversial, not least because it could also facilitate dispersal of hyperparasites which would counter the effects of the parasitoid on the host population.

However, introduction of natural enemies against exotic aphids in Australia is by no means a new tactic. Wilson (1960) recorded interstate transfers of wasps from 1902 and introductions from Europe from 1903 against the black citrus aphid, *Toxoptera aurantii*. The wasp *Aphelinus mali* was introduced against the woolly apple aphid, *Eriosoma lanigerum* (a North American species), in 1923. Maelzer (1981) noted that there are few generalised parasitoids of aphids in Australia and many aphids then had no parasitoids recorded in Australia. Some of those studied appear to have little effect on the host populations: *Diaeretiella rapae* parasitises the cabbage aphid, *Brevicoryne brassicae*, but has little impact on at least some populations (Hughes and Gilbert, 1968). Maelzer advocated introduction of both specific and polyphagous parasitoids against aphids. Carver (1988) also recommended that 'gaps in the aphidiids [i.e. wasp parasitoids] should be filled and selected parasites introduced' against further aphid pests, such as cereal aphids, and one of the most important disease vectors, *Myzus persicae* (Fig. 20). The wisdom of this approach is discussed in Chapter 6. Other early introductions of parasitoids against aphids were made against the oak aphid, *Myzocallis annulata*, a pest of ornamental oaks, and the pine aphid, *Chermes boerneri*, a pest of young *Pinus radiata*. Wilson (1960) summarised releases against these made in the 1930s.

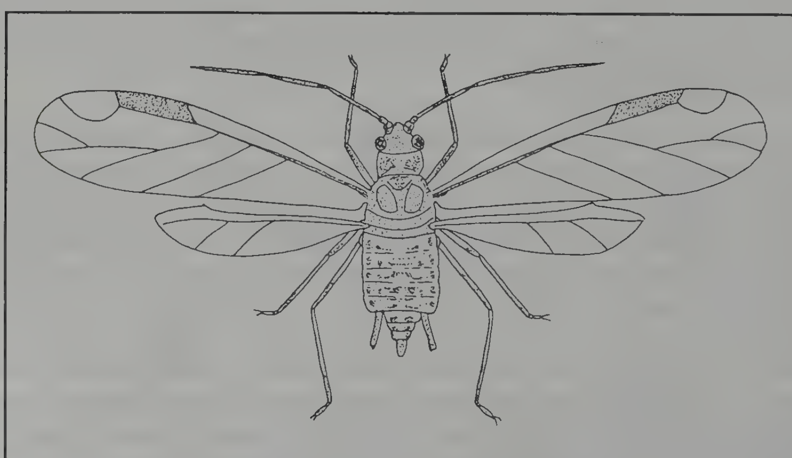

Fig. 20. A representative exotic aphid, the peach aphid, *Myzus persicae*.

A rather different kind of aphid attack in Australia, and one which has had significant effects on the development and maintenance of an important industry, involves a native North American species which infests vines, viz. the grape phylloxera, *Daktulosphaira vitifolii*. It became a devastating vineyard pest in France, where it was overcome largely by utilising resistant rootstocks to which the desirable grape varieties were grafted.

Phylloxera first appeared in Australia (at Geelong, Victoria) in 1877 (Buchanan, 1987) and later infested several other wine-growing areas. Because the aphid is dispersed easily on plant material, quarantine measures preventing spread of grapevines were instituted early, and since 1900 control has been through use of resistant rootstocks derived from American vine species (Buchanan and Hardie, 1978). Although quarantine measures generally contained phylloxera for about 75 years, recent surveys (Buchanan, 1987) showed it to be present in 41 of 281 vineyards surveyed, with recent expansion of the grape industry serving to increase the total infected area substantially from 1902. Only a small proportion of vines were from grafted rootstocks, which are more expensive and require more attention than ungrafted vines (Buchanan and Godden, 1989). Clearly, phylloxera has persisted in Victoria at several locations.

Cabbage white butterfly. The cabbage white (or small white) butterfly, *Pieris rapae*, rapidly became a serious pest of cabbage and related cruciferous crops in all States after it first appeared in Victoria in 1939. In addition, it is a frequent pest of garden-grown vegetables of this category. Native to Europe and northern Asia, this species is also widely distributed in North America and is thought to have arrived in Australia from New Zealand (Jones, 1981), probably on vegetables on ships. It reached other States (except the Northern Territory) by 1945, and rapidly became the target of biological control attempts. The pupal parasitoid wasp *Pteromalus puparum* was imported from New Zealand and liberated initially in Victoria (1941) and Tasmania (1942); it was distributed through other States by 1945 (Wilson, 1960). Two species of larval parasitoids, *Apanteles glomeratus* and *A. rubecula* (both now placed in the genus *Cotesia*) were also introduced in the 1940s, and together the three can provide substantial levels of biological control. Caterpillars are also susceptible to a granulosis virus, though apparently this is not as important as it is in Europe. The larvae of *P. rapae* can feed on a wide range of crucifers, including a number of widespread and common weeds, so that it is not truly dependent on crops but is able to invade these easily, often from nearby 'reservoir' populations. The searching behaviour of adult females for host plants on which to lay has been studied intensively (Jones, 1977, 1981) and *P. rapae* is clearly a highly dispersive species able to search effectively for suitable plants.

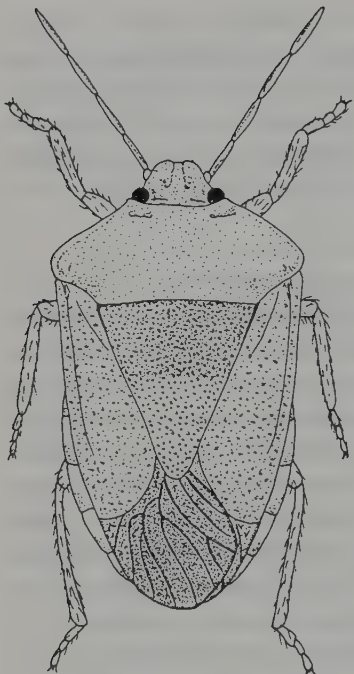

Fig. 21. The green vegetable bug, *Nezara viridula.*

Green vegetable bug. The green vegetable bug, *Nezara viridula* (Fig. 21), has been so widely dispersed throughout the world that its original home area is not known with certainty. It can be a serious pest of many ornamental plants and of crops. For Australia, Waterhouse and Norris (1987) listed the following as attacked: peas, beans, other legumes, cucumbers, potatoes, tomatoes, passionfruit, groundnuts, sorghum, soybeans, sunflowers, tobacco, maize, crucifers, spinach, lucerne, grapes, oranges, and macadamias. It was first reported from Australia in 1916, and biological control using a small scelionid wasp egg-parasitoid (*Trissolcus basalis*) was initiated in 1933. Other species of *Trissolcus* have also been introduced, and different strains of *T. basalis* from different climatic regimes led to more effective control over much of the bug's Australian range. *Nezara* is thus at present a relatively infrequent pest, though occasional damage occurs, especially on the subcoastal areas of northern New South Wales and southern Queensland.

Because *Nezara* is so widespread, there are now numerous locally adapted strains of *T. basalis* in various parts of the world, so that there is considerable potential for continuing to utilise others as they are needed and, whilst such diverse introductions serve to increase the genetic diversity within an exotic parasitoid species, no further parasitoid species may be needed. Waterhouse and Norris (1987) emphasized that any use of chemicals for other pests on plants where *Nezara* is being controlled may reduce the level of biological control achieved.

However, Clarke (1990) believed that the claim that *Nezara* is under good biological control by *T. basalis* in Australia might be poorly founded and based on circumstantial evidence in some instances. Other wasps are undoubtedly contributors to the bug's mortality, but the bug's main period of decline (hailed as a biological control success) also coincided with widespread use of synthetic insecticides in the 1950s and 1960s.

Pea weevil. Changes in commercial emphasis or in the area grown of different crops often leads to expansion or decline in importance of associated pests. During the last few years, the area of field peas grown as a winter crop in rotation with cereals in southern mainland Australia has expanded greatly, from a grain pea yield of 33,000 tonnes in 1983 to 487,000 tonnes in 1987. In association with this industry growth, pea weevil (*Bruchus pisorum*: Fig. 22) has increased in importance to become the most significant pest of peas. Adults of this European beetle hibernate and migrate to invade crops from the edge in spring. Weevils lay their eggs on young pods and the larvae bore through the pod wall and into seeds to the extent that more than 70 per cent of seeds may be infested in high rainfall areas. *Bruchus pisorum* thus causes substantial yield loss and is a significant contaminant of export grain (Smith, 1990). Control of the weevil is therefore important in two different contexts.

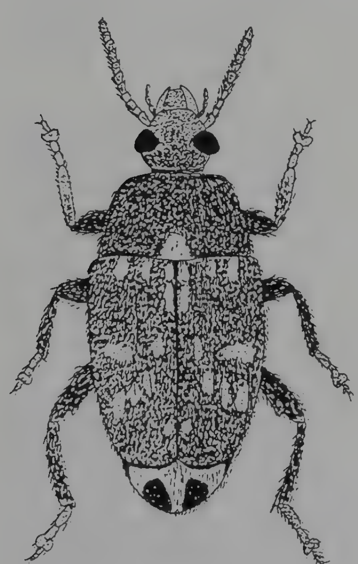

Fig. 22. The pea weevil, *Bruchus pisorum*.

Control has traditionally been by chemical means, and optimal timing and application has involved spraying the perimeters of the crop over the period that adults invade. Dispersal of weevils further than 30–40 m into the crop is slow (Baker, 1990), so that such border sprays can

be very effective. Multiple spraying may be necessary for dense weevil populations. Two European wasp parasitoids, one attacking eggs (the trichogrammatid *Uscana senex*) and one affecting larvae (a braconid, *Triaspis thoracicus*), might be candidates for importation as biological control agents; however, they have not yet been studied sufficiently to assess their suitability, although this is regarded as priority for refining control of the pea weevil. Once infested peas have been harvested, with early harvest recommended as a tactic to help manage field infestations, fumigation of the stored grain may be needed. Adult weevils may emerge over a period of nine months. Early fumigation is recommended (Williams, 1990) and either methyl bromide or phosphine may be employed.

Weed control

Prickly pear. The biological control campaign in Australia against prickly pears (*Opuntia* spp.) is one of the great classical successes of the biological control of weeds, and provided impetus for much further work against other weeds. The campaign has been documented extensively (Dodd, 1940, 1959; Wilson, 1960; Clausen *et al.*, 1978) and is recapitulated only briefly here, reflecting that it occurred during a period when biological control was a much less sophisticated science than it is today, and many of the refinements now commonplace in screening candidate insects for release were not routine procedure.

The several species of *Opuntia* are all North American. Two, *O. inermis* (common prickly pear) and *O. stricta* (spiny prickly pear), were particularly aggressive weeds in Australia and spread rapidly in areas where they had been planted as hedges or potential fodder crops. Some 24.3 million ha of land (about 80 per cent of it in Queensland, the rest in New South Wales) was infested by 1925, about half of it as very dense growth which excluded more desirable fodder grasses and other plants. In only the next 15 years, this massive infestation was dramatically reduced by a large biological control campaign which involved insects imported from North America, Argentina and South Africa. Most stands were destroyed by the late 1930s, and the Commonwealth Prickly Pear Board (founded in 1920) was consequently disbanded in 1939. The policy of this Board included a thorough survey and study of **all** insects attacking prickly pears and other Cactaceae in America, and the selection, importation, release and distribution of candidate biocontrol agents. The initial pool of about 150–160 insect species was narrowed to 50–60 species sent to Australia, of which about 12 were finally established (Table 6).

The major decline of *Opuntia* was attributed directly to a small phycitine moth from South America, *Cactoblastis cactorum*. However,

Table 6. Insect species established in Australia as potential control agents of *Opuntia* spp. From Wilson (1960).

		Source	To	Dates
Lepidoptera				
Cactoblastis cactorum	(Phycitidae)	Argentina	Q, NSW	1926–1933
Tucumania tapiacola	(Phycitidae)	Argentina	Q, NSW	1935–1939
Olycella junctolineela	(Phycitidae)	USA: Texas	Q, NSW	1924–1927
Coleoptera				
Moneilema ulkei	(Cerambycidae)	USA: Texas	Q, NSW	1926–1939
M. variolare	(Cerambycidae)	Mexico	NSW	1932–1934
Lagochirus funestus	(Cerambycidae)	Mexico	Q	1936–1940
Hemiptera				
Chelinidea tabulata	(Coreidae)	USA: Texas	Q, NSW	1922–1929
C. vittiger	(Coreidae)	USA: Texas, Florida	Q, NSW	1925–1929
Dactylopius opuntiae	(Dactylopiidae)	USA, Mexico	Q, NSW	1921–1926
D. newsteadi	(Dactylopiidae)	USA: Texas	Q, NSW	1925–1926
D. ceylonicus	(Dactylopiidae)	Argentina	NSW	1935
D. sp. nr *confusus*	(Dactylopiidae)	Argentina	Q, NSW	1933–1937

Dodd (1959) believed that control would have been achieved even without this agent because several other introductions from 1913–1914 (such as *Dactylopius* spp. (p. 28), coreid bugs (*Chelinidea*) and a lepidopterous borer (*Olycella*)) had increased considerably in the field and were causing local thinning and destruction of both species of *Opuntia*. Intriguingly, *Cactoblastis* was also introduced in 1913–1914, but a colony could not be established (Wilson, 1960). However, the story was different by 1925: a single consignment of 2,750 eggs sent from Argentina to Brisbane were cultured in the laboratory for two generations to give a 900-fold increase in numbers. Well over two million eggs were liberated in 1926 and releases from the laboratory stock continued until the end of 1927. By that time, nine million eggs had been distributed in *Opuntia* areas of Queensland and New South Wales. Dispersal was aided further by collecting eggs from field populations and spreading them further afield. The establishment of *Cactoblastis* was completed by 1931. Around 4 million larvae/ha were needed to destroy dense *O. inermis* stands, but more than 95 per cent of the 20 million ha of *Opuntia* in Queensland had been wiped out by 1940, giving virtually complete biological control, and other agents decreased in importance because of competition from *Cactoblastis*. In contrast, resistant forms of both *Opuntia* spp. occurred in New South Wales, mainly as chlorotic 'yellow' varieties. By increasing nitrogen supply, in some areas by killing nearby standing timber, the plants were made much more susceptible. At present the *Cactoblastis-Opuntia* system is an 'almost classic two-species interaction with little interference from predators or competitors' (Monro, 1975).

An exotic Acacia. The most speciose plant genus in Australia is *Acacia* (Mimosaceae), with nearly 1,000 species. It is important as the host plant of large complexes of Australian endemic insects. However, an additional *Acacia (sensu lato)* species from India and Pakistan (*A. nilotica indica*) was introduced into Queensland early this century as a shade tree. It has since become a weed as it forms very dense prickly thickets which interfere with stock mustering. It was spread extensively through growth from seeds passed in cattle dung and was declared a noxious plant in 1959. Biological control has recently been investigated (Willson, 1985), and the predominant agent released was a seed-boring beetle, *Bruchidius sahlbergi*. After assurance of its safety, more than 300,000 beetles were released at 96 sites in 1982–84 and *Bruchidius* rapidly became established in many places. Liberations were mainly on trees near permanent water to ensure that sufficient seeds were available.

This agent is of particular interest in Australia, where Bruchidae (or Chrysomelidae: Bruchinae) are not diverse. Predispersal seeds of Australian acacias are attacked heavily by weevils (Curculionidae) but, apparently, not by native bruchids. About 100 weevil species are known from *Acacia* in Australia. Lack of bruchids on Australian acacias is regarded as an ecological peculiarity. It remains to be seen if *B. sahlbergi* may eventually change hosts and interfere with native weevils.

St John's wort. St John's wort, *Hypericum perforatum*, is a pest of pastures in summer rainfall areas of temperate Australia, as well as in parts of Canada and the United States. It is particularly abundant in Victoria, where it occupies large areas of (particularly) sheep-grazing country. *Hypericum* is toxic to sheep and an aggressive competitor with more desirable plants. Biological control was pursued first in Australia with initial exploration in Britain in 1928, and the first introductions of potential control agents were made in 1929. Seven agents had been liberated in Victoria and/or New South Wales by 1940, and a gall midge (*Zeuxodiplosis giardi*) was released in the early 1950s (Wilson, 1960).

Four of these did not become established. The two most important were leaf-beetles, *Chrysolina quadrigemina* and *C. hyperici*, both of which became very abundant, and which were distributed to the other southern States. Their success in controlling *Hypericum* (mainly by *C. quadrigemina*) was viewed as partial. In general, control was better in more open ground and beetles did not control *Hypericum* effectively in wooded areas. They were used in combination with herbicides and pasture improvement. The beetle thus seemed to function as a factor contributing to plant stress rather than as a full solution to the weed problem and its long term association with *Hypericum* in Australia has been studied extensively (Briese, 1985). Despite reaching very high numbers periodically in high

summer rainfall areas, *C. quadrigemina* seemed unable to control the weed, prompting renewed attempts at biological control from 1979. *Hypericum* has also continued to spread in Australia and the apparent need was for agents which could stress the root reserves by summer feeding. An aphid (*Aphis chloris*) and a noctuid moth (*Actinotia hyperici*) were released in the 1980s. The programme is continuing. Laboratory studies on the aphid (Briese, 1988) and predictive models for its performance in the field (p. 84) suggest that it is likely to be a successful agent. Although other species of *Hypericum* support development of *A. chloris*, these are not at any substantial risk in the field and the aphid is not a risk as a virus vector to non-host plants (Briese, 1989).

Aquatic weeds. Two important aquatic weeds have choked water-bodies in Australia through their vigorous growth. Salvinia (*Salvinia molesta*) and water hyacinth (*Eichornia crassipes*), both from South America, are major pests of water-bodies in tropical and subtropical regions, and salvinia occurs also in some temperate areas. Both were apparently introduced as aquarium plants, *Eichornia* about 1894 but *Salvinia* not until 1952. However, by the late 1970s, the latter was already the more widespread (Waterhouse and Norris, 1987). Salvinia is a floating fern and in Australia both weeds have been controlled by weevils introduced from South America. *Cyrtobagous salviniae* was released in June 1980 on Australia's largest salvinia infestation (Lake Moondarra, Queensland). The initial release of about 3,000 insects increased to an estimate of more than a hundred million in less than a year! Within that period, virtually complete destruction of an estimated 10,000 tonnes of salvinia on the lake occurred (Room *et al.*, 1981, 1984). Weevil larvae tunnel into the rhizomes, where they progressively destroy nodes, internodes and even roots (Sands *et al.*, 1983). Other releases in Queensland were also very successful and the weevil has now controlled the weed elsewhere in Australia as well as in other countries such as Papua New Guinea, India and Sri Lanka. A second agent introduced against *Salvinia* was a foliage-feeding lepidopteran, *Samea multiplicalis* (Pyralidae). Because of infestation of the imported stock with a microsporidian disease, release was delayed in an attempt to eliminate this in laboratory cultures. The moth became established rapidly once released. Despite rapid natural spread (up to 200 km in about two and a half years; Julien *et al.*, 1984), it has little real impact on the weed, but does not interfere with the performance of the weevil (Forno, 1987).

Successful control of many water hyacinth infestations has been due to the weevil *Neochetina eichorniae*. As in the case of *Salvinia*, the weevil proved to be far more effective than a moth, in this case *Sameodes albiguttalia*. Part of this difference was apparently because young caterpillars are not able easily to enter leaves through the hard epidermis.

Chapter 6

Exotic Insects and Conservation Concern

Predicting spread and change of exotic species

In Chapter 2, the ecological characteristics of a species that tend to render it a successful coloniser or invader were noted and the difficulty of making any universal generalisations was stressed. Predicting success or failure of a deliberately introduced insect is clearly of great practical value, but several other relevant aspects of how exotic species fit into their new environment are difficult or even impossible to assess before they are introduced. The most important of these themes are: whether they will spread extensively, especially into natural habitats; if so, what factors will limit or restrict their spread; and whether the organism will change to include genotypes far different from those of populations in the areas of origin.

Each of these topics is complex, as discussed by Andow *et al.* (1990). These authors showed that the spread of an exotic species may depend on a number of species and population characteristics. These include: whether range expansion occurs in many short steps (that is, by gradual expansion) or fewer, larger ones; whether the population achieves a constant rate of spread and, if so, whether this can be related to local demographic and behavioural factors; and how spread may be affected by variation in habitat quality. Resolving any of these questions necessitates research at several scales in order to relate local events to intrusion into a larger geographical area, as well as correlation of species features with those of the receiving environment.

All of these aspects have ramifications for assessing and predicting environmental impacts of the species in the new area (for example, as causing conservation concern or in predicting the effectiveness of biological control agents). In terms either of anticipating problems or of predicting successful control of important pests, any estimates of these traits are highly relevant. Available knowledge of a species' biology and environmental tolerances can sometimes be integrated to assemble models to predict resource suites or climatic regimes which might restrict or determine the distribution of the species or the limits to its spread. The reliability of this approach necessitates understanding which factors determine a species' distribution. Climate, for example, may not be

limiting, although it is often assumed to be so, and considerable emphasis has been placed on predicting the optimal climatic regimes for a given insect to thrive.

One approach, pioneered in Australia as CLIMEX and BIOCLIM (Table 7), is to attempt to assess climatic requirements, predominantly as limited by temperature and precipitation (Busby 1986). Based on tolerances and rates of development under a range of conditions, climatic optima for a given species can be defined, sometimes within rather narrow limits. The CLIMEX programme (Sutherst and Maywald, 1985) utilises known climatic data about the regimes experienced by an insect in its native range and cross-matches this to Australia to indicate how severely a pest may infest, or how successful a control agent may be and where each might establish or be introduced if these climatically optimal conditions do not change. It may then be possible to project the optimal needs to a geographical region to define areas where the species could thrive and secondary areas where it might be self-sustaining but at a lower level of success. In CLIMEX, separate indices can be derived to show how a population may grow in a particular area and how a species might persist through a climatically unfavourable period. These two measures combine to give an Ecoclimatic Index, expressing the locality's suitability. A slightly different suite of climatic features was used by Burt *et al.* (1976) to predict performance of tropical pasture plants introduced to Australia: latitude, altitude, the number of months giving 85–92 per cent of total rainfall, the highest monthly maximum temperature during the wet

Table 7. Summary of characteristics used in BIOCLIM (Bioclimatic prediction system). From plotted distributions of species, the BIOCLIM system can be used to determine distribution limits of species by showing areas with similar climate to the known distribution. Characteristics after Busby (1986).

(i)	Mean temperature (annual)
(ii)	Minimum temperature (of coldest month)
(iii)	Maximum temperature (of hottest month)
(iv)	Annual temperature range (difference between above two)
(v)	Mean temperature of wettest quarter
(vi)	Mean temperature of driest quarter
(vii)	Mean precipitation (annual)
(viii)	Precipitation (of wettest month)
(ix)	Precipitation (of driest month)
(x)	Annual precipitation range (difference between above two)
(xi)	Precipitation of wettest quarter
(xii)	Precipitation of driest quarter

season, the lowest monthly minimum temperature during the wet season, the same temperature measurements during the dry season, and average annual rainfall.

Consider the possible practical inferences from the examples of introduced dung beetle (p. 56) distributions in south-eastern Australia shown in Figs 23–25. Here, the triangles show where successful releases have been made, and the open circles indicate areas climatically suitable for the

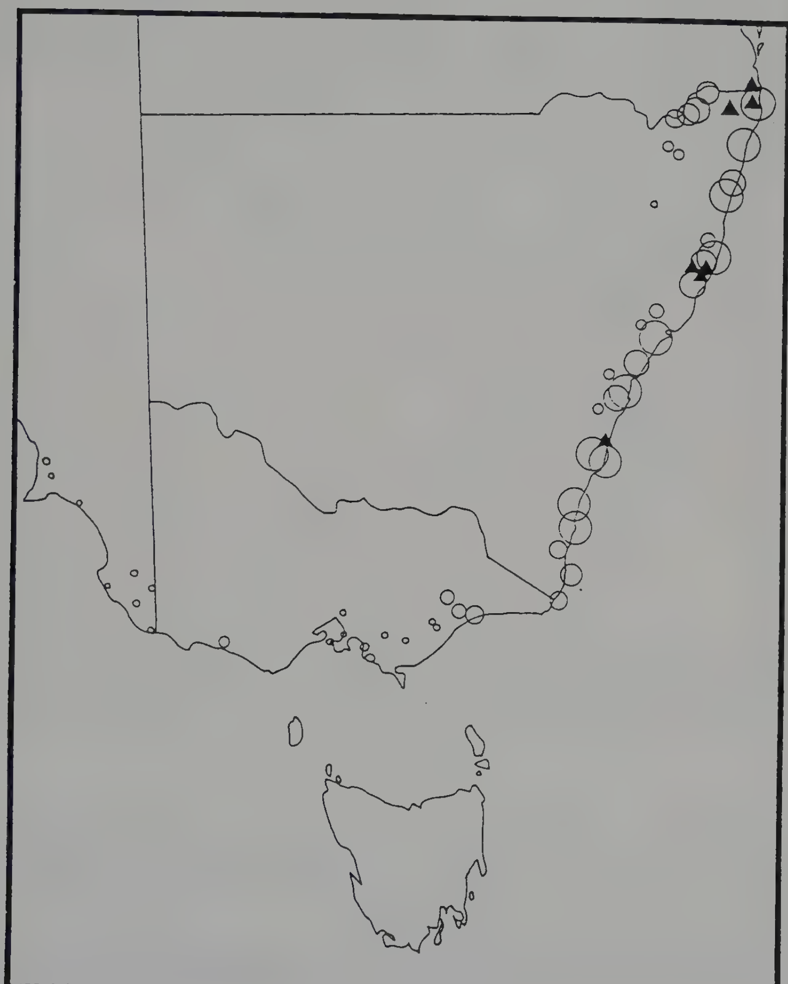

Fig. 23. CLIMEX diagram indicating the potential range of exotic dung beetles released in south-eastern Australia. The larger the circle, the more suitable the area; triangles indicate sites of introductions. This diagram shows the potential (and actual) range of *Onthophagus nigriventris*. After Tyndale-Biscoe (1990).

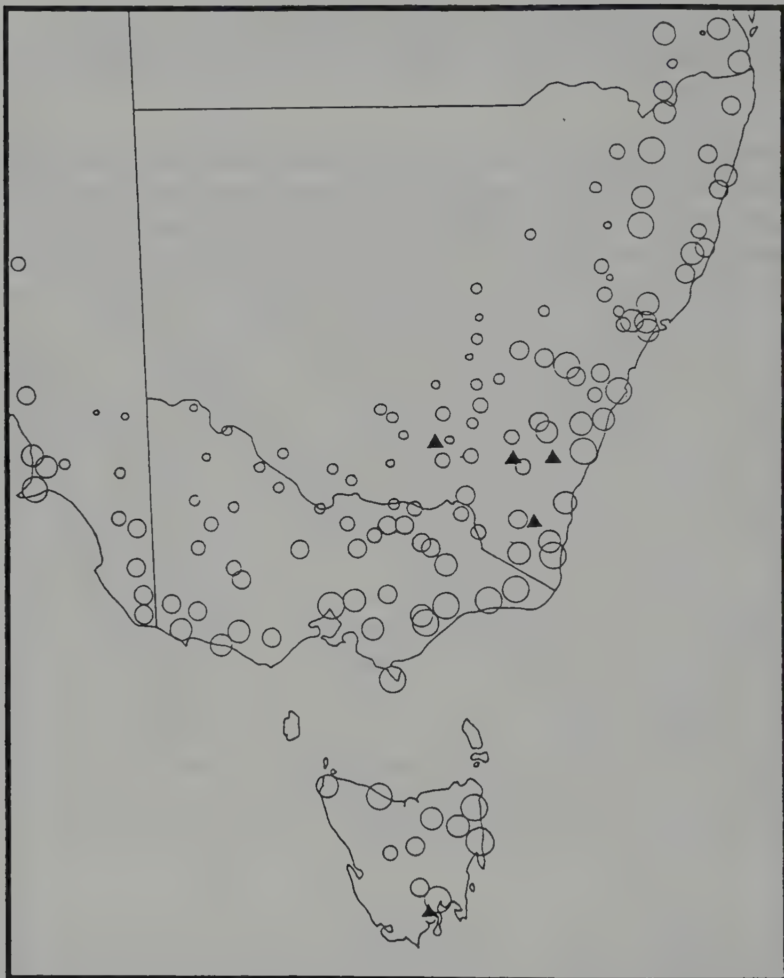

Fig. 24. CLIMEX diagram for *Geotrupes spiniger*. See legend to Fig. 23 for further explanation.

beetle, with larger circles denoting higher suitability than smaller circles. *Onthophagus nigriventris* (from high rainfall areas of East Africa) would essentially be confined to coastal regions and could not tolerate the warmer drier inland regions to any significant extent. However, the large circles indicate that it could probably build up large populations, especially along the southern coast of New South Wales. By comparison, *Geotrupes spiniger*, which is widely distributed in Europe, is ecologically much more tolerant and could thrive as a useful dung control agent over much of the south-east (including Tasmania). It is still not able to function satisfactorily in the inland, and probably not as well as *O. nigriventris* on the east coast. As a third example, also from Tyndale-Biscoe (1990), *Onitis alexis,*

from southern Europe and much of sub-Saharan Africa, has already been established widely in New South Wales and its potential for further spread in this area is rather limited. The southern limit of this species seems to be defined by the inability of the larvae to survive wet winters, rather than any effect of temperature (Tyndale-Biscoe, 1988). Such comparative information is invaluable in planning future priorities for distributing biological control agents to new areas where they could be effective—a process often involving considerable logistic commitment in collecting, receiving and transporting stock and releasing it safely. In this instance, the data imply that investment in distributing *O. alexis* further southward would be markedly less rewarding than concentrating on *G. spiniger*, and that *O. nigriventris* merits spreading along the New South Wales coast.

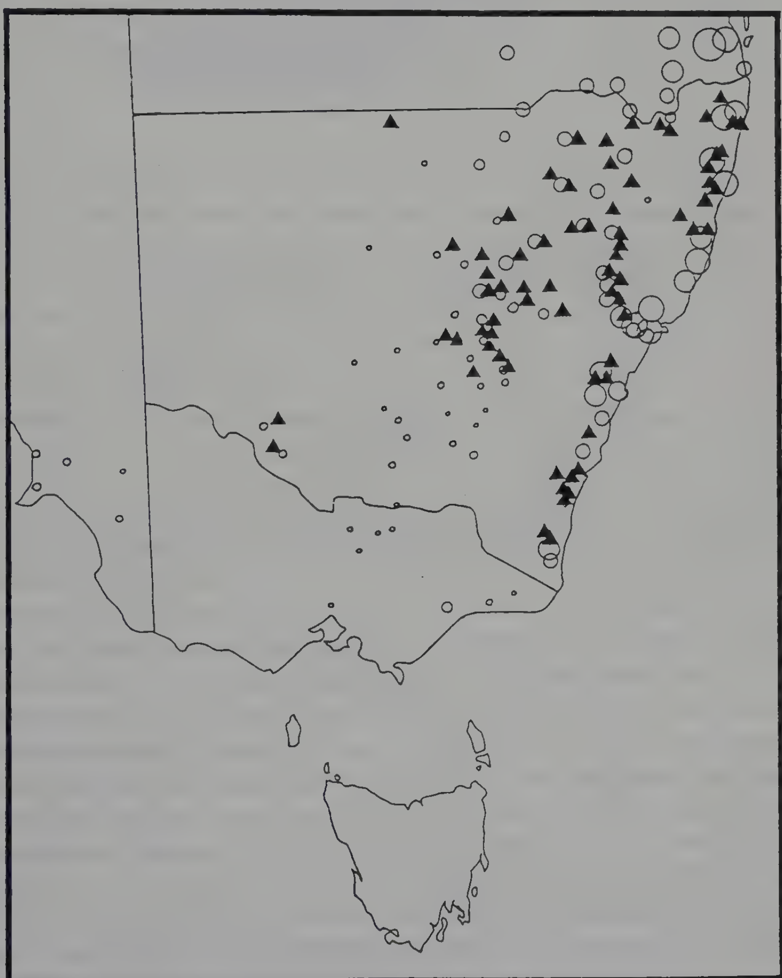

Fig. 25. **CLIMEX** diagram for *Onitis alexis*. See legend to Fig. 23 for further explanation.

Other information, such as the growth rates of the agents, is also relevant, of course, but much futile work can be saved and complementation releases planned soundly on CLIMEX information or similar programmes. Equivalent data are usually not available for less economically-significant exotic insects, but the above examples stress that subtle patterns of distribution are likely to occur, and that predicting the performance of one species even from data derived from an ecologically similar close relative is not likely to be reliable, even in very general terms. Probably, most insects likely to invade natural ecosystems are restricted by the need for such optimal climatic regimes to provide conditions which give them the greatest likelihood of overcoming biotic resistance as they invade, as well as by more obvious resource needs. One aspect of the intrusion of social insects into natural systems is that their mode of existence, in enclosed colonies, helps to buffer them from some climatic extremes and this may facilitate their expansion into a wider range of environments than might be accessible easily to many solitary insects.

If sufficiently reliable laboratory data are available on development rate in relation to temperature, it is possible to model the anticipated performance of an agent after release in more detail. Fig. 26 shows, for example, the number of generations which the aphid *A. chloris* could undergo each year in various parts of southern Australia in conjunction with its target, St John's wort (p. 76) (Briese, 1988). The range calculated was 8–25 and normal climatic variation and scale effects would ensure some differences between sites. However, the method is apparently reliable for making such broad-scale estimates.

The potential for adaptation of an exotic species in a new environment can also be related to its genetics, reflecting its adaptive flexibility and, hence, its variability. It is usually not clear whether the genotype of a species in a new area differs substantially from that in its parent population but often it is reasonable to presume some change, as a result of taking a small subsample of the parent population or later selection. Founder populations of an exotic insect may be small, or biological control agents may have been selected from a small part of their natural range (perhaps that which is most compatible climatically with the intended area for release) or mass-reared to select for particular favourable traits. Natural selection in the new area is also likely to induce genetic change. Murray *et al.* (1986) noted that populations of some insect biological control agents (such as *Cactoblastis*) differ genetically between Australia and the South American source populations, and that different populations in Australia are also distinct. The full significance of such differences is by no means clear. In some instances, agents have been distributed extensively from an area where they are introduced. Wilson (1965) noted

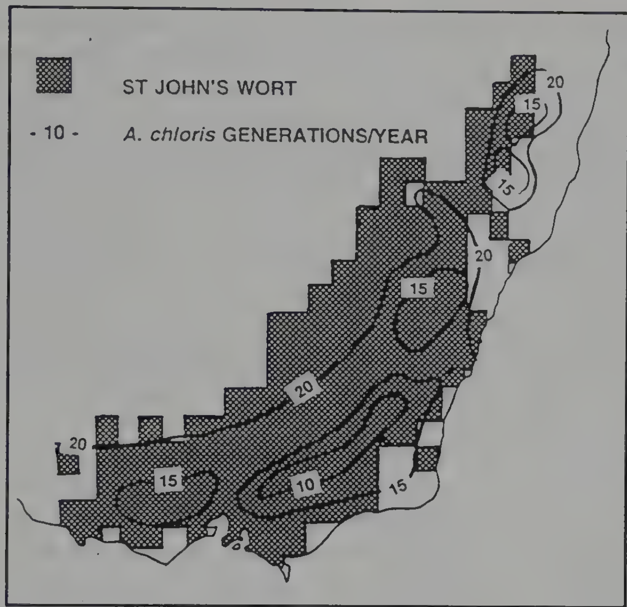

Fig. 26. *Aphis chloris*: predicted number of generations in the field. The shaded area indicates distribution of St John's wort (*Hypericum*), isoclines, the numbers of generations/year of the aphid (10, 15, 20). After Briese (1988).

the example of *Chrysolina quadrigemina* (p. 76, introduced to Australia from France for biological control of St John's wort). Material of the beetle from Australia has been introduced subsequently to various parts of North America, New Zealand, South Africa and Chile, each introduction constituting a further sub-sampling of the parental natural population.

In this beetle, genetic variation manifests as a colour polymorphism; beetles may be bronze, green, purple or blue, or some intergrade between these. Wilson (1965) suggested that changing proportions of the various colour morphs might reflect changing genetic make-up of the *Chrysolina* population and reflect adaptive traits and environmental suitability. Later work on this species, which clearly relates colour differences to differences in fitness, emphasises that the ecological genetics of this system merit far more attention (Murray, 1985).

Part of the rationale of classical biological control is often to select in the laboratory for the most appropriate strain of an agent for release in a particular area, so exploiting the natural variability of the agent population. It is clearly important that an insect introduced deliberately should be pre-adapted to that environment. This pre-adaptation can

sometimes be enhanced during very few laboratory generations, so that, for example, strains of parasitoid Hymenoptera capable of tolerating relatively extreme environments or with greater reproductive potential have been sought. Such efforts run counter to the philosophy of introducing the greatest genetic variability and allowing the 'fittest' to develop through natural selection after release. This can take time to manifest: *Chrysolina* seemed to disappear and die out soon after its liberation in Australia (1939), but reappeared in abundance in 1942 and thereafter stayed common. Wilson (1965) suggested that this period could have reflected selective mortality involving the various colour morphs noted earlier. Such examples provide valuable information for understanding adaptive changes and evolution in new environments.

The genetics of colonising species, especially that seeking any possible generalities which distinguish them from non-colonisers, has received considerable attention in recent years, with the premise that a new environment can constitute stress with which a low population has to contend. A changed genetic environment can lead to maladaptation. One consequence of a small population (or bottleneck) phase in a species' colonisation sequence may well be a decline in viability through enforced or unusually high inbreeding. This principle has been discussed widely in conservation management, where the aim of safe-guarding small populations incorporates preventing the loss of genetic variability and preservation of diversity. There is little practical difference between a population of a species reduced to small numbers in its original habitat (unless this is due to destruction of that habitat so that it has no realistic potential for recovery) and one in small numbers needing to exploit a new habitat: each situation constitutes a classic bottleneck through which the species has to pass if it is to succeed. The genetic ramifications are discussed in several texts (Ford, 1975; Parsons, 1983; Hoffman and Parsons, 1991; and especially clearly by Frankel and Soulé, 1981). Inbreeding may lead to depression of fitness through loss of genetic variation and there may be no 'safe' level of inbreeding for normally outbred organisms. One possible trait, as sought for biological control agents, is relative uniformity, but this may be countered by their being highly sensitive to environmental variations because of reduced tolerance of extremes. Many insects have much greater genetic variation (as evidenced by variation in biochemical characters such as enzymes and other proteins shown by electrophoresis) than vertebrates. Extensive laboratory experiments have shown that in *Drosophila* (among the best-studied of all animals in this context) variation is indeed related to 'fitness' and coping with environmental variation. Small populations may respond slowly to natural selection, so that lack of variability may well affect the rate of evolution in a closed environment. However, it is extremely difficult to demonstrate that lack of variation ever becomes limiting for an insect.

A new environment provides forms of stress (Parsons, 1987; Hoffmann and Parsons, 1991) for a small population.

Development of genetic protocols for captive-reared insects for release, either as an adjunct to conservation through re-inforcing or translocating populations, or as biological control agents, needs much further attention, as stressed by Roush (1990). For insect control agents of weeds, Murray (1985) contrasted two alternative strategies related to interaction of genetic features with a change of environment. If the receiving environment resembles that of the source population, it might be better to (1) mix individuals from different sources, (2) maintain these as a large stock which is not permitted to adapt to artificial rearing conditions, and (3) make a few releases, each of many individuals. This procedure may conserve genetic variability and avoid inbreeding depression. For a receiving environment which differs substantially from the original one, a preferable strategy might be to (1) take a small founder sample from a single source population, (2) expand this quickly in the new environment, and (3) either separate it into many distinct lines soon after release or establish many initial lines each from a small sample. This might result in extinction of most of the populations released but the survivors should be well adapted to the new surroundings. These hypotheses need to be tested experimentally (Roush, 1990).

In comparison with the original distributions, a small colonising population often is distinguished by distinct phenotypic factors or biological characteristics, reflecting a small founder gene pool. In addition, mutational events may permit additional adaptive potential, and recent work (discussed by Parsons, 1987) suggests that stress conditions could result in increased genetic variability. The amount of work needed to determine whether or not successfully colonizing species have any unique or peculiar features of genetic architecture is enormous: Parsons (1983, 1987) discussed some possible avenues for advancing understanding in this field, namely, comparative studies of cosmopolitan and narrowly endemic *Drosophila* species. But 'ultimately...experiments should have a high priority...because there is no other way of making reasonable, scientifically based recommendations about these aspects of colonisation' (Roush, 1990).

In any discussion of exotic insects, some reference to the rapidly-developing field of genetic engineering and the release of genetically modified organisms (GMOs) is pertinent, not least because this is receiving considerable attention in Australia and frequently evokes public alarm over perceived risks such as 'killer bees' and the like. A GMO, even of a native or naturalised species, is novel and constitutes a new biological entity in the environment. Unlike other kinds of modified organisms, such

as domesticated animals and crops (in which selection for particular desirable features is usually associated with the loss of many wild traits), splicing genes into an organism to breed a population with enhanced ability in a given feature does not eliminate wild traits—hence the derivation of such terms as superorganism, beloved of press reporters. Some form of risk equivalent to that of introducing a true exotic species may be feared from GMOs, and many of the relevant concerns were discussed by Regal (1986) and for Australia in a recent Parliamentary Report (House of Representatives, 1992). Regal pointed out that, of a number of models and approaches projected to try to understand GMOs, the lessons from introduced species are particularly pertinent, both for the difficulty of seeking generalisation, so that each needs to be studied as an independent case, and because the risks are sufficiently low that no overall moratorium is warranted as long as each case is assessed properly.

Any exotic species constitutes *per se* a change to the environment it enters. That change, as discussed in earlier chapters, may be regarded as beneficial, harmful or (commonly) of little consequence. Further entries, such as the importation of biological control agents to counter exotic plant or animal pests, enhance the complexity of an exotic community. Especially in disturbed environments, such species tend to enter habitats similar to those whence they came. Genetic change may then be minimal, and enhances adaptation at the local level. Elsewhere, the species may appear to be a more aggressive invader and intrusion into natural (or relatively undisturbed) habitats can cause concern. This usually does not arise until the insect is well established, perhaps abundant, there; occasional individuals of particularly notable taxa (such as *Vespula* wasps) may evoke comment but many others intrude less conspicuously. In general, there is no monitoring of undisturbed habitats in Australia to detect invasions by exotic insects or other invertebrates. Lack of funds and adequately-trained personnel ensure that this state of affairs will continue. Nevertheless, some early warning of such intrusions by selected exotic species known to be established in fringe habitats (see Chapter 2; Povolny, 1971) could indeed be a valuable adjunct in conservation procedures in Australia.

Charles Elton (1958) was among the first of modern ecologists to express vividly the potential unifying effects of exotic species when he likened the main biogeographical regions of the world to water tanks with interconnecting taps. Flows, representing the movement of exotic species, and interchanging between different parts of the world (water tanks) might eventually erode the unique biota of each region and increase the homogeneity and faunal similarity between them as more and more animal and plants become widespread or cosmopolitan. This might be viewed as a highly exaggerated claim because many exotic biota are

restricted to modified environments, the culture steppe, and do not invade natural regions; even so, the rapid intrusions of plant weeds and feral mammals in many parts of the world, and notably into formerly pristine Australian ecosystems, has ominous forebodings of Elton's concern. This chapter indicates some of the relevant concerns arising in Australia through the advent of exotic insects.

Fears have been expressed for the safety of native biota in the face of invasion by exotic insects, especially those which do indeed disperse into undisturbed environments, and our lack of ability to counter such harmful intrusions. Commenting on exotic invertebrate invaders in Hawaii, Howarth (1986) wrote: 'Our ecological experience is not yet sophisticated enough to propose specific, environmentally sound measures for most problems concerning alien invertebrates'. This applies also to most other countries. A general feature of many exotic species is that they may become extraordinarily abundant, far more so than even closely related native species, and some may lead directly to change in natural communities through competitive aggression. This is best documented for social Hymenoptera (*Vespula* in New Zealand; Thomas *et al.*, 1990), and instances described in several other parts of the world are directly relevant in Australia (they sometimes even implicate the same species), for which primary studies are limited or non-existent. However, in general, competitive exclusion is very difficult to demonstrate unambiguously. On continental-sized land masses, Herbold and Moyle (1986) suggested that exotic and introduced species might co-occur for long periods, perhaps even centuries, before competitive exclusion would result in extinction of one. Most exotic species have been present in Australia for short periods, not more than several decades, so such potential effects would not have been realised yet.

The Argentine ant (p. 56) in Australia is not a rapid natural invader, because flight is limited and many new nests are formed within walking distance of the parent colony. Its rapid spread in the United States has been associated with ant transport in merchandise, perhaps especially by train, but it is regarded as extraordinarily aggressive as a coloniser (Elton, 1958). In North America, it spreads fast and destroys virtually all native ants in the colonised areas (Smith, 1936). This trait was evident also in Australia and, in both countries, control and removal of *Iridomyrmex humilis* was followed rapidly by the reappearance of native species. Imported Fire Ants (*Solenopsis invicta*) in the United States were also successful competitors against native species (e.g. Porter *et al.*, 1988), and this pattern is seemingly not uncommon among introduced ants. Indeed, *S. invicta* also replaces *I. humilis* in North America. According to Porter *et al.*, (1988), replacement of colonies of the native *S. geminata* by *S. invicta* (polygynous form) represents a radical restructuring of an

arthropod community. The invasion process continued for a substantial period in an area by budding from early colonies well after the main invasion front had passed. *Solenopsis invicta* can also have major impacts on populations of both invertebrates and vertebrates, including reasonably large ground-nesting birds whose nestlings they eat (survey by Lofgren, 1986). Because such ants are omnivorous, they have also been hailed as beneficial in some places as they prey on pest insects on crops. Such ambivalent or contradictory roles are more common among biological control agents than is generally acknowledged (below), and evaluation of their status is usually appraised in relation to short-term control needs with little regard for longer-term intrusive effects.

A further effect of *I. humilis*, signalled by its invasion of fynbos vegetation in South Africa, where it also displaces native ants, is its reduction of recruitment into populations of many native plants (Bond and Slingsby, 1984). There, as in Australia (Berg, 1975), myrmecochory—the transport of seeds by ants—is widespread. Argentine ants do not fill this role and loss of specialised seed-dispersing ants results in markedly reduced germination.

Another aggressive, introduced ant is the now widespread tropical big-headed ant, *Pheidole megacephala*. This probably originated in the African region but now occurs throughout much of the Pacific area. As with many of the other widespread insect invaders discussed here, its effects are more obvious in island environments; in Hawaii, for example, Howarth (1986) categorised *Pheidole* as a 'notorious nectar robber' which would aggressively defend food resources and deter other species from using flowers. However, it is known to compete with native ants in Australia. Majer (1985) studied the return of native ant species to rehabilitated sand mine sites on North Stradbroke Island, Queensland, and found a linear pattern of ant return to about 24 species after about seven years (Fig. 27). On older plots (8, 10, 15 years), there was a sharp decline of native ant species, associated with *P. megacephala* colonising the mine site and reaching very high densities.

Vespula wasps have been studied far more extensively in New Zealand than in Australia, and the subtle and complex ecological effects that are gradually being documented there are a salutary warning of likely parallels in Australia in the future. 'The potential ecological impact of the wasps has been signalled for many years...but these effects are only now being quantified' (Sandlant and Moller, 1989: New Zealand). The wasps compete with native nectar-feeding birds for sugar resources, for example, and have been implicated directly in the endangerment of an endemic parrot, the Kaka (*Nestor meridionalis*) (Beggs and Wilson, 1991). In *Nothofagus* forests, a major source of food (and, thus, of energy) for the

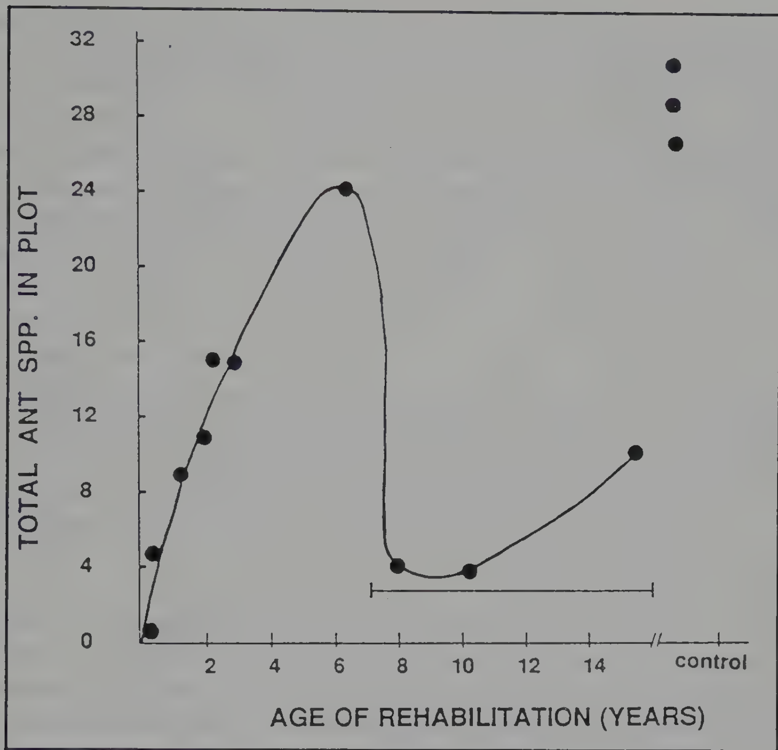

Fig. 27. The big-headed ant, *Pheidole megacephala*: competition with native ants on North Stradbroke Island, Queensland (Majer, 1985). Relationship between return of ant species to plots and incidence of *P. megacephala* (horizontal line, from year 7) shown. After Majer (1985).

parrots is honeydew produced by a scale insect (*Ultracoelostoma assimile*). This is greatly reduced by being eaten by *V. germanica* and *V. vulgaris*. Densities of up to 283 wasps a square metre of honeydew-infested bark have been recorded in late summer and autumn (Moller and Tilley, 1989). Biomass estimates of *V. vulgaris* gave levels higher than the combined biomass of birds, rodents and stoats, for example, in a beech forest in the South Island (Thomas *et al.*, 1990). As well as reducing the number of drops of honey dew, they induce a decline in the energy value per drop. Kaka were absent when the wasps were abundant, and Beggs and Wilson believed that for about four months of the year the presence of wasps reduced the supply and quality of the honeydew to the extent that it was no longer a viable food resource for the parrots, affecting their supply of high-energy food in late summer and autumn and reducing their breeding fitness for the following spring. As well as involving Kaka, the honeydew is an important food for native honeyeaters, tui (*Prosthemadera*), bellbird (*Anthornis*), and silvereyes (*Zosterops*) (Clout and Gaze, 1984).

The effect of such wasps as generalist predators may also be significant and this aspect, also, has not yet been appraised in Australia. Davis (1978) noted that most such wasps can be considered beneficial because they may feed on pest insects. However, as with others, the converse effect may be engendered if they feed on native insects. Concern has been expressed, for example, about *V. pensylvanica* preying on endemic arthropods in Hawaii (Gambino *et al.*, 1987). The wasp was apparently introduced to Hawaii on Christmas trees imported from the mainland of North America. A number of local endemic species on Maui (where the wasp first appeared in 1978) were captured by wasps at high altitudes on Haleakala (Gambino *et al.*, 1990) and they were seen to pose a threat to these. As with related species in Australia, establishment of perennial colonies was likely to augment this threat considerably because of the vast numbers of wasps seeking animal protein. In New Zealand, wasps were noted to kill many invertebrates to feed their larvae, probably indeed a sufficient number to limit the food supply of insectivorous birds (Sandlant and Moller, 1989).

Harris (1991) intercepted returning wasp foragers at their nests in parts of the South Island of New Zealand and found about 15 per cent (1,190/8,002) with animal prey, including nine orders of insects and several of Arachnida. Quantification of this led Harris to suggest that wasps consume a prey biomass of similar order (8.1 kg/ha/season) in northern South Island in summer-autumn to the entire bird fauna for the year. Estimates for western South Island, in contrast, were only 1.4 kg/ha, but a reduced habitat carrying capacity for insectivorous birds was likely when wasps were present.

Some of the concerns over the roles of feral honeybees in Australia were noted earlier (p. 25). Competition between honeybees (including both apiary and feral stocks) and native insect pollinators is still an open question, but one which is being addressed actively. There are also concerns over whether native birds, particularly honeyeaters, may be disadvantged by nectar depletion by honeyeaters, a topic discussed in detail by Paton (1993).

Many conservationists believe that there is sufficient likelihood that harmful effects are occurring that apiarists should not be permitted to site hives in or near National Parks and other reserve areas where sensitive native fauna may flourish. Foraging range for a colony can extend to many square kilometres (Roubik, 1989), though most foraging is much closer to the nest. It has also been suggested that feral bees should be eliminated progressively from such regions both because of the nuisance they may cause around camp sites in arid areas as they seek water, and also because they may occupy some of the limited supply of tree-holes and similar nest

sites which would normally be used by parrots or mammals and, thus, reduce the effective populations of these.

Sugden and Pyke (1991) believed that even relatively low densities of feral honeybees could lead to changed foraging patterns of a native bee, *Exoneura asimillima*, and that a high density of apiary bees would have intensified effects. Food storage, with resultant competition for nectar, was a possible cause of this adverse interaction.

Conflict of interest

An important suite of conservation concerns arises from the deliberate introduction of exotic insects for biological control, and several recent essays have addressed this, either generally (Samways, 1988) or in the more specific context of small isolated islands such as Hawaii (Howarth, 1983, 1991) and Guam (Nafus, 1994). Both levels of concern are relevant to Australia, an isolated island continent with a highly endemic fauna of a similar nature to those which have been eliminated on small islands by the effects of introduced predators and parasitoids nominally specific to particular target pests and which have moved to attack other prey or hosts. As Harris (1988) stressed, the goal of biological control is indeed to change the composition of biota in a given region—in his context of weeds, to change the local composition of plant species by decreasing weed abundance. It is thus inevitable that some ecological impact occurs and (again from Harris, 1988) that impact is desirable if most people like it! For weeds, concern is frequently expressed that introduced insect control agents will attack non-target plants, including rare and desirable native species, once the weed has been reduced to short supply. Such plants, though, may simply be too rare to sustain populations of the insect consumer, and there is no evidence of extinctions of plants caused by biological control agents (Harris, 1988).

Whatever tests are employed to ensure and demonstrate that a given consumer is a feeding specialist and **not** likely to transfer to other plants (or, in other contexts, other hosts or prey), concern over the possibility of such transfer tends to remain, even though it may be highly infrequent. The safety record of insects introduced to control weeds is extremely good; Lawton (1985) summarised data to estimate that an insect used in a biological control programme had a probability of only $1x10^{-8}$–$1x10^{-7}$ species/plant species/year of unexpectedly switching to a non-target species. A host transfer in this context usually means the additon of another host rather than the abandonment of their usual one. Some purists thus tend to oppose the use of classical biological control on the grounds that no absolute guarantee of safety can in fact be made. In

discussing more general disruption of communities by introduced species, Pimm (1989) noted three scenarios where impacts might be especially severe:

(1) species being introduced into places where predators are absent might increase their impact (desirable for biological control);
(2) introduction of polyphagous species; and
(3) species introduced into relatively simple communities: the removal of only a few plant species might result in collapse of the communities.

Care is certainly needed when deliberately introducing any such exotic species, even though they may be entirely successful biological control agents. Even *Cactoblastis* (p. 74) larvae were found eating melons and unripe tomatoes once their *Opuntia* food supply started to decline (Dodd, 1940), and the coreid *Chelinidea* used against *Opuntia* ate a range of different fruits under those circumstances. Neither of these associations has persisted, and they seem to have been transient or 'casual' range expansions of superabundant populations with declining normal foodstuffs.

It is incumbent on a country importing a biological control agent to ensure that it is **likely** to be safe, but such matters of public interest are inevitably difficult to assess. The Australian Biological Control Act (1984) (stimulated by the controversy over biological control of *Echium*, p. 97, and court cases arising from this) ruled that biological control can be used for a weed only if it is likely to achieve control of the target species, and that it must be likely that the insect (agent) will cause no harm to the environment or to people. If harm **is** caused, it must be less than that occurring if biological control is not used at all. This condition, means in principle that some unwanted ecological effects may be acceptable if they are less than the consequences of other forms of weed control or of not controlling the weed and allowing it to spread (Cullen and Delfosse, 1985; Harris, 1988).

Samways (1988) noted that biotic contamination by classical biological control agents is likely to be irreversible, but that in practice the risks of contamination must be balanced against the certainty and reality of pest devastations. Alternative control methods may give increased risk of pesticide contamination, though this is most commonly restricted largely to the vicinity of the target. Exotic biocontrol agents are almost always introduced with the aim of reducing intrusion or impact of target species which are themselves exotic, and agents may thus be the lesser evil.

Introductions of polyphagous natural enemies have occurred on numerous occasions in the past: Wilson (1960) and others noted a number of instances involving, for example, unidentified ladybirds and green lacewings. Taylor (1979) noted that endemic *Sensoriaphis* spp., some of

the relatively few native Australian aphids, might be affected by generalist predators which had built up numbers in response to exotic aphids, but the evidence for this is by no means clear. *Sensoriaphis* tend to breed later than the exotic aphids, and such predators have been found in their colonies after the spring collapse of exotic hosts.

There are thus two distinct areas of concern over exotic insects introduced as biological control agents:

(1) that they may extend into natural environments and expand their feeding range to encompass non-target, possibly rare, native taxa; and

(2) that the programmes which allow such agents to be introduced are sometimes not necessary or advisable because, as the target is beneficial to particular sections of the populace, control should not be undertaken.

The first of these concerns addresses mainly non-specific predators and parasitoids of insects, some of which could even attack other biological control agents in the same system. For Hawaii, Howarth (1983) recapitulated Zimmerman's earlier belief that importation of parasitoids to control economically important moths had resulted in the loss of many endemic species of Lepidoptera. In turn, reduction of native caterpillars may have led to rarity, even extinction, of some native predators such as *Odynerus* wasps. Later workers (cited by Howarth) indicated that this decline of native arthropods in Hawaii was a prime factor in the ensuing decline and extinction of some native insectivorous birds. The large number of generalist hymenopterous parasitoids introduced to Hawaii has made it very difficult to utilise introduced Lepidoptera as herbivores to control exotic weeds there, according to Howarth (1983, 1991). However, the above effects may not have been due entirely to biological control agents, because habitat destruction and chemical applications have also proceeded apace in Hawaii. Even so, Coulson and Soper (1989) strongly agreed with Howarth's emphasis on the needs for more post-release evaluation studies of natural enemies. However, competent and complete **pre**-release evaluation may be, this cannot be a substitute for **post**-release appraisal.

Equivalent effects of biological control agents have not been confirmed for Australia but the above scenario indicates possible concerns which could apply. Taylor's (1979) comment on decline of native Australian aphids, noted above, emphasises the need for continuing vigilance and monitoring of introduced predators and parasitoids which could probably transfer to other hosts. The ability of an agent to disperse actively is viewed as a desirable characteristic (p. 38) as long as it remains in association with its target and does not expand its food spectrum, especially

through intrusion and establishment in more natural areas where its original target might not occur.

A few instances have been reported where introduced natural enemies have indeed attacked other biological control agents: examples are given by the wasp *Trichogramma minutum* in Hawaii (introduced for control of agricultural moth pests and implicated in the failure of an introduced moth to control nutgrass); a gall fly introduced to Hawaii to control *Eupatorium* is attacked by parasites introduced to control fruit flies; and the ladybird *Cryptolaemus montrouzieri* introduced to South Africa as a predator of pest mealybugs also attacked *Dactylopius* introduced to control prickly pear there. These and other cases are documented by Bennett (1985). He also noted the case of commercially desirable birdwing butterflies in Papua New Guinea, which could involve very close scrutiny of proposals for biological control of any weed related to their larval foodplants in areas where butterfly ranching is being fostered as a cottage industry. Some parasitoids proposed for introduction to control sugarcane borer moths (*Chilo*, Pyralidae) had to be tested to ensure that they would not affect butterfly caterpillars.

Dangers of weed control agents to rare plants were discussed by Harris (1985). Circumstances which could give rise to concern were a combination of three conditions:

(1) the plants occurring in the same area as a common host plant target;
(2) the plants are accepted readily by the consumer; and
(3) they support good survival of the consumer.

In general, it seems that this combination would be extremely rare and, even then, a rare (possibly, endangered) plant may not be discovered by a herbivore: its very rarity might prove to be a refuge and constitute protection from a new consumer entering the natural community of which the plant is a minor part. It is also usually difficult to isolate biological control as the influencing factor, as noted above for Howarth's island moths. As examples (cited by Harris, 1985), many plant species may be at risk from herbicides in Germany, and biological control might result in overall reduced herbicide use, so more species would be saved than placed at risk; and competition by the introduced weed may itself threaten other plant species in its new community.

More frequent conflicts of interest arise over whether to attempt biological control of a target plant which is a pest in one region but desirable (or a close relative is) in another, or where the target has weed and commodity status to different people. Such conflicts can be protracted and costly, and may be very difficult to resolve. One such example in Australia has been blackberry (*Rubus fructicosus* agg.), for which an exotic

insect, a stem-boring sawfly (*Hartigia albomaculatus*: Cephidae), and a rust fungus (Uredinales) were investigated as likely control agents. Opposition to this control programme in south-eastern Australia came from apiarists, pickers and canners of wild berries, and growers of *Rubus* crops (Field & Bruzzese, 1985). Blackberry value for the apiary industry was highest in Tasmania, with relatively little on the Australian mainland. Collection of wild blackberries, mainly for jam manufacture (where they are used as a blend with cultivated berries), is declining but, together with berries picked by people for home consumption, was still worth several hundred thousand dollars annually in Victoria and Tasmania. Concern from crop growers was mainly over the likely specificity of the rust. Conflict over this case was pre-empted by the apparently deliberate and unauthorised release of the rust in Victoria, where it spread rapidly, aided by further illegal human transport of infected foliage. Although this case is not centred primarily on exotic insects, it is one of the few recent instances in Australia in which an exotic agent has indeed been deliberately established without full prior clearance to do so, and thus evidences concern over its possible repetition, perhaps indeed involving insect agents, in the future.

By far the best known and most important biological control conflict in Australia has been over *Echium plantagineum*, the naturalised plant known as Paterson's Curse or Salvation Jane—the very names reflecting the dichotomy of opinion over its prime role.

A biological control programme against *Echium* was commenced in Australia in the early 1970s, and 11 species of insects from the western Mediterranean were selected as potential biological control agents. Four of these were imported in 1979–80 (Delfosse, 1985): a leaf-mining gracillariid moth (*Dialectica scalariella*), two flea beetles (*Longitarsus aeneus*, *L. echii*, the adults of which feed on or in roots), and a stem-boring cerambycid beetle, *Phytoecia coerulescens*. The seven others were two sap-sucking Hemiptera (Tingidae), a shoot and flowerbud-feeding moth, two flower-feeding beetles and two crown-boring weevils, so that the various species seemed likely to complement and compound each other's effects to produce substantial mortality of the plant. However, an injunction to prevent biological control of *Echium* was sought by the apiary industry (the four plaintiffs included two apiarists and two graziers), and an interim injunction (10 July 1980) included agreement that CSIRO would not release or import any further agents (Cullen and Delfosse, 1985). This came at the time that *D. scalariella* was already being mass-reared to build up stocks for release, and most of these had to be killed. The laboratory colony of *P. coerulescens* was also destroyed, during a critical phase of investigation when attempts to mass-rear it on an artificial diet were nearing completion.

The benefits of the plant were seen, broadly, as three-fold: a provider of a significant proportion (10–15 per cent) of the national honey crop and a source of nectar and pollen for bees early in the season; a useful forage plant for stock at times when little other feed is available; and an aesthetic attraction when flowering. The undesirable (weed) features are: the presence of toxic or carcinogenic alkaloids; an aggressiveness, hindering and outcompeting more desirable pasture plants, leading to decreased nitrogen input to the soil; poor forage qualities; the pollen is a significant allergen and contributor to hay-fever; and the difficulty of controlling it with herbicides such as 2,4-D (Cullen and Delfosse, 1985).

At the time of the injunction there was no mechanism in Australia whereby a biological control agent which could disadvantage any individual or sector of the community could be released. Protracted debate resulted eventually in such enabling legislation: the Biological Control Act 1984 initially applied only to the ACT but State legislations later extended its impact. Biological control of *Echium* was recommended to commence again by an Inquiry in 1985. The Act has had far-reaching consequences for the prosecution of biological control in Australia, where it covers all relevant programmes.

Many pest insects on crops tend to become the focus of attention soon after they arrive in a new area, as their effects are conspicuous and/or economically damaging. The date of their arrival can often be inferred within rather narrow limits. Several of the aphid pests noted earlier, for example, had their arrival chronology fixed to within a few months because of the data provided by continuing surveys of aphids over much of south-eastern Australia and designed to detect those very events. For many innocuous insects, the time of arrival is much more uncertain; although they may be discovered suddenly, they may in fact already have been present for a considerable period so that their rate of invasion is not clear.

A European moth whose small caterpillars feed as miners inside the foliage of exotic ornamental oak trees was recorded in Canberra in 1976 (Common, 1977). This moth, *Phyllonorycter messaniella*, was by then abundant on several species of *Quercus*, including both deciduous and evergreen species. It was known in New Zealand from the early 1950s (Wise, 1953) but had not been noted previously in Australia. Its discovery in Canberra prompted searches in several other southern capital cities, where it was also found commonly. Both in Canberra (Common, 1977) and Melbourne (New, 1981) it had established to the extent that it was being attacked by several Australian parasitoid species. In south-eastern Australia, the moth occurs commonly with most species of *Quercus*, but causes little public comment although densities may exceed 20 mines/leaf

in some places. Surveys of the 'Oak Lawn' of the Royal Botanic Gardens, Melbourne, show that it has changed little in abundance there during the last decade and significantly that many (?most) of the numerous visitors do not notice the foliage blemishes there. Such species are the so-called silent intruders, difficult to document fully except by rare chance and, in general, innocuous for most of the time, though occasional outbreaks may be more conspicuous and demanding of attention. Some, such as the elm bark beetle (p. 63) have potential to cause more significant damage.

Similarly, there is very little clear idea of the country of origin for some exotic species in Australia, including some which are important crop pests. This circumstance is not a problem for stored products pests, for example, but can be a disadvantage for any insect for which classical biological control is contemplated, because the initial search for suitable natural enemies has conventionally occurred within the natural range of the host. Seeking these in areas in which the pest itself is exotic may yield only an atypical or biased subset of those which may be available, even though some are likely to be found. The diamondback or cabbage moth, *Plutella xylostella*, is now virtually cosmopolitan, but is believed to be native to southern Europe. It is a frequent pest of brassica crops, where young caterpillars mine foliage and window the leaves. It is a multivoltine species and insecticides and biological control have both been used to attempt to reduce populations to less than damaging levels.

The various wasp parasitoids employed against *Plutella* in Australia date from 1902 (Western Australia) or the mid 1930s–1940s (most other States). Collectively, these were imported from England, Italy, Spain, India, Sri Lanka, China or New Zealand (records in Waterhouse and Norris, 1987), and the many levels of field parasitisation recorded range up to about 70 per cent (near Sydney in 1971–72). In Queensland in particular, the parasitoids do not always reduce *Plutella* populations adequately. Overall, the parasitoid guild associated with *Plutella* in Australia is quite diverse (nine species near Melbourne, for example, Goodwin, 1979) and both superparasitism and hyperparasitism may reduce their effects.

The values and roles of urban tree planting have been promoted extensively in the recent planning of urban expansion in Australia and in moves to beautify inner urban areas of several capital cities. Elsewhere, a wide range of benefits have been noted. These range from important counter-pollution roles such as absorption of carbon dioxide, production of oxygen and adsorption of dust (Root and Robinson, 1949) to physical and biological values such as windbreaks, noise buffers, erosion controls, shade provision, light buffers (such as by reducing glare of vehicle headlights), fire buffers, deceleration barriers, attractants for birds and mammals, and

hosts for beneficial insects (list after Olkowski *et al.*, 1978), as well as trees being, simply, ornamental. Traditionally in Australia, exotic trees have been used in urban areas more than native species, though this trend is now reversing. Urban trees may commonly host exotic insects which may be pests (elm leaf beetle, p. 64), generally innocuous (oak leaf-miner, p. 98), or potentially serious as vectors of diseases which could destroy the trees (elm bark beetle, p. 63).

Chapter 7

What next? Prediction and Regulation

Introduction

In late April 1992, a woman tourist returned to Australia (via New Zealand) from South America with a wound in her neck which contained maggots of the New World screwworm fly, *Cochliomyia hominivorax*. This was the first incidence of this species in Australia, and, if it became established it would represent an immense threat to the livestock industry. The related Old Worm screwworm (p. 41, 112) is one of the most feared insect potential invaders of Australia. Slightly earlier, in February 1992, a bumble bee, *Bombus terrestris*, was found in Hobart, Tasmania, and further sightings in 1993 indicate that it has established in the area; it was probably introduced accidentally from New Zealand.

Many further species of insects will eventually arrive from overseas. Likewise, existing populations of some exotic insects have the potential to be augmented regularly from overseas and these arrivals are difficult to document even though they may have considerable practical importance.

The yellow fever mosquito, *Aedes aegypti*, was probably introduced first to Australia around the middle of the nineteenth century (Lee *et al.*, 1987). It became quite widespread in eastern Australia both by internal transport from Queensland—such as on trains, as it breeds mainly in small artificial water-bodies including (then) station fire buckets and train toilets (which have probably aided substantially in transporting the species inland)—and by multiple arrivals by sea. It breeds in rainwater tanks, discarded vehicle tyres and other similar habitats in the warmer parts of Australia and is important as the only known vector in Australia of the virus causing dengue fever; it also carries several other pathogens. The history of *Aedes* spread in Australia is discussed extensively by Lee *et al.* (1987). Dengue fever was first reported from Australia on a ship arriving from Mauritius in 1873. It was well established in Darwin during the second world war (Whelan, 1984). In the Northern Territory, the mosquito has tended to increase in abundance away from Darwin and to decline in towns, the former trend reflecting an increase in numbers of rainwater tanks and the latter related to the advent of reticulated water systems to replace such tanks. There is potential for dengue fever to re-establish in the Northern Territory and the mosquito has been found

breeding in water containers on boats entering Darwin from Indonesia. Continuous surveillance for *A. aegypt* occurs in the area and arriving boats are checked for mosquito eggs. This is viewed as a necessary strategy to counter dengue fever, for which the virus could be imported in people and transmission then be effected rapidly by *A. aegypti*.

Australia is well placed to receive many important insect disease vectors imported in aircraft. Many have also been distributed in this way to other parts of the Pacific (Laird, 1984) and the need for effective quarantine to monitor and control this trend is indeed strong.

Quarantine

The concept of quarantine measures to prevent ingress of exotic organisms or disease is an ancient one. The term was applied initially to the 40-day period of isolation applied to ships arriving in European ports from a country where endemic diseases occurred, to allow for incubation and prevention of those, and the word (quarenta is 40 in Italian) is derived directly from this. Nowadays, quarantine implies the regulatory strategies (under such names as Plant Quarantine or Plant Protection) used by many countries as a strategy against exotic pests, pathogens and weeds. There are three main areas of application (Kahn 1989), namely:

(1) the exclusion of exotic organisms, undertaken by an importing country to protect itself from pest establishment;

(2) phytosanitary certification and/or treatment of (usually, agricultural) exports, carried out by an exporting country, normally at the request or requirement of the importing country to aid the latter in pest exclusion. For Australia, for example, there is a requirement for wood products to be fumigated prior to shipment and importation; and

(3) plant protection, essentially domestic quarantine to control recently introduced organisms in the above categories which have not yet become widespread.

There are numerous differences between countries in the applied details, effectiveness and efficiency of prosecution of these activities and in the extent and reliability of quarantine legislation. Insects are thus only one component of quarantine activities, albeit an important one which is difficult to monitor effectively.

Almost all the insects which are considered of quarantine significance are those associated with plants and plant products (either causing direct damage or being vectors of plant diseases) or those which transmit human or animal diseases. Other than biological control agents, higher

level consumers are of relatively little significance, but the profile of generalist predators in quarantine considerations seems likely to increase as their potential environmental roles become better known. Procedures for such species do exist (see discussion by Coulson and Soper, 1989). Insects are named in the quarantine regulations of most countries: a 1986 listing of plant pests (Holdeman, 1986) recorded 408 genera and 663 species of significant insect taxa. The roles and importance of many intercepted insects are not known, and the quarantine rationale generally adopted is to err on the side of safety: when in doubt, keep it out. Overcoming the vast knowledge gap to obviate this ignorance is a massive problem which is unlikely to be solved fully in the foreseeable future. In general, meaningful quarantine criteria can be developed only for taxa whose identity is clear and whose biology (including economic or medical impact) is reasonably well known. Assessing risk, even for these, can be difficult. For many others, it is impossible, and both short-term and long-term applications may be needed (Kahn, 1989). Quarantine procedures have biological considerations and logistical constraints: both are important for such generally inconspicuous organisms as insects.

The example of timber-boring insects mentioned above demonstrates some of the difficulties involved for a group of insects whose undesirability is generally accepted and for which most or all species found are potentially harmful. Virtually all are imported with wood rather than being naturally highly dispersive, and four kinds of commodities constitute avenues for importation (Wallenmaier, 1989), namely, logs, lumber, wooden packing materials, and living plants. Logs commonly have the bark attached and, especially if they are allowed to remain in the forest after felling before shipping, they may harbour many species of insect. The term lumber refers to trimmed or sawn timber, such as the majority of Asian rainforest woods imported into Australia. Insect infestation may be less in this than in logs because of bark removal and the fact that the wood is in smaller pieces. Packing material, ranging from pallets to crates, is used for a multitude of imported manufactured goods. Imported trees may easily harbour the early stages of wood-boring insects and are subject to very close inspection. Unlike many other guilds of insects, the long period which timber may pass in ships' holds or on decks is not usually a hindrance to immigration, because timber insects tend to have long life cycles or can build up numbers in the timber utilised by their parents. Wallenmaier (1989) made the sobering point that any two countries which trade regularly with each other have probably established inadvertently a conduit for wood-borers in packing materials.

The problems of designing and implementing quarantine measures against insects reflect many aspects of insect biology and diversity, from their small size and the inconspicuousness of many immature stages and

their resilience (through periods of dormancy) to the stresses of normal travel, to the difficulties of identification and recognising those which may be significant. As well as detecting the actual insects (or fragments of them), quarantine officers may need to recognise and associate such clues as faeces, egg shells, cast larval skins, pupal cases, silken webbing, holes in plants, seeds or timber, and blemishes on foods or plants. Effective inspection, therefore, cannot be superficial as it might have to encompass seeking insect eggs on dormant nursery stocks, pupae in soil, contaminants in sacking, beetles in grain or seeds, and many other locations where highly cryptic organisms may be present in small but significant numbers. Identification of these is essential in order to assess their roles and to determine what (if any) regulatory action may be needed. A series of criteria to determine quarantine significance can take into account any known impacts of the insect—an evaluation of the potential pest status in the quarantining country (Kahn, 1989). These can be refined by incorporation of further biological data as these become available and by weighting the various criteria to emphasise those believed to be the most significant. A given insect may be accorded high quarantine status if it is known to cause economic damage elsewhere, for example, or if it could have detrimental environmental impact. Using an example of insects associated with cut flowers imported into the United States, Kahn (1989) illustrated three levels of significant interception along lines of much broader application:

(1) highly significant (insects identified to species, known to have high potential to become a serious pest, usually with at least a moderate potential to colonise after spreading from cut flowers, or with a lower potential to cause economic damage but a high potential to colonise);
(2) least significant (identification only to family or genus because of the life stage found, but a high potential of being a pest already widespread in the area of introduction **or** with very low potential to colonise or to cause economic damage); and
(3) moderately significant (any not fitting the two categories noted above).

Biological information regarded as important criteria in assessment even in this single context included host range and plant availability, seasonal synchronisation, availability of and the insect's need for mates, the time available for colonisation until the cut flowers are discarded, the intended use of the flowers (inside or outside), developmental stage of the imported insect, and relative numbers (high or low) of individuals in the shipment. These criteria must be related to local conditions, so that a tropical pest may not be able to survive in cool temperate latitudes if it were imported, or a pest under glasshouse conditions may not have this status on field-grown plants, and so on.

Socioeconomic criteria may be employed, such as the acreage and value of host crops, and suites of these and biological features can be combined in models to determine and rank the quarantine significance of insects.

One model, which has been discussed extensively and is summarised by Kahn (1989), arises from a report by Daum (1978). It is illustrated here (Fig. 28) to exemplify the kind of multi-criterion quarantine index which can be constructed. The Daum model evaluates three socioeconomic criteria and four biological criteria. The former, based on available agricultural data, are expressed in logarithms, and the latter are evaluated on a scale of 1 to 10. Socioeconomic criteria are: the economic

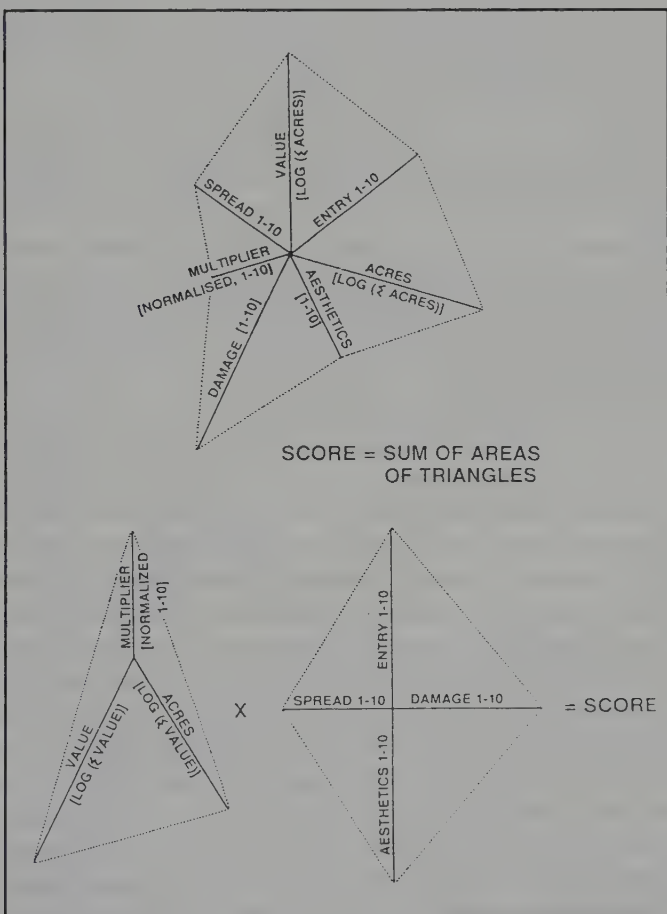

Fig. 28. Development of a quarantine ranking system including biological and socioeconomic criteria for exotic insects. From Daum 1978, in Kahn (1989). See text for explanation.

(farm) value of the host crop; a 'multiplier effect' value (converting farm value to off-farm value, so including manufacture, processing and other costs); and number of acres of the host crop. Biological criteria are: the potential of the insect to cause damage; its ease of entry; its potential rate of spread; and adverse aesthetic or environmental impacts. These can be combined to form an area polygon in which increasing area is equivalent to increased importance for quarantine. Economic criteria tended to overshadow biological data, and the two sets of criteria can be plotted separately if necessary to form a triangle plus a four-sided polygon whose areas are multiplied to give a ranking score if one wishes to combine these complementary criteria.

Accurate identification to species level is critical to effective implementation of quarantine against insects. For exotic arrivals, rather than for local or domestic quarantine, the three main needs (modified from Foote, 1978, discussing the United States) are:

(1) interceptions at ports of entry. This may include exotic species from any part of the world. Information on their place of origin and their economic importance there is needed, and identification may need to be as precise as possible (rather than just 'aphid' or 'grasshopper');
(2) new pest detection, with similar requirements to the above; and
(3) insects not known to occur in the importing country. This is most important for the few hundred pest species of economic importance and, again, species-level identification and characters differentiating it from close relatives may be needed.

A survey of experienced insect systematists working in the United States National Insect Collection (Knutson, 1989) showed the need for greatly increased resources to provide the capability to identify insects as reliably as possible and the constraints on doing this at ports of entry by non-specialist workers. For many insect groups, including some of very high economic importance, the information needed is simply not available. There are few (if any) taxonomists working on them and support for increasing their number and providing logistic support for them is unlikely to be forthcoming. Well-curated reference collections and identification guides which are sufficiently detailed and well illustrated to be intelligible to non-specialists are usually unavailable. The continuing problem that about half (at least) of all insect species have not yet been named formally ensures that difficulties in definitive recognition will persist. Identification of any reasonably unusual import may demand considerable original research to give the correct name, even for an insect species which has been described. Many people do not realise this and nor that it may be quite misleading to apply the 'nearest available name' in an identification because this might dramatically misrepresent the insect's biology and economic or social importance. Even a formalised 'diagnostic

service' (such as those operating in Canada, the United States and the United Kingdom) is likely to have major gaps in its coverage and abilities simply because of limitations in expertise and personnel.

The practical ramifications of this state of affairs are enormous and, in extreme cases, could mean that quarantine laws cannot be enforced, pest species could be permitted entry, or permits to enter harmless goods may be denied. However, practical quarantine measures are commonly more focussed. Later (p. 111) several pests which could be expected to arrive in Australia are noted and these may act as foci for quarantine inspections. Early detection of exotic pests (p. 117) is a major factor in facilitating early and efficient control or eradication measures. A need for very precise identification can be obviated by ranking particular insect kinds containing pest taxa high on quarantine schedules: the United States thus includes 'Senn pest complex' (*Eurygaster integriceps* s.l., Heteroptera) and 'Weevil' (Curculionidae) on schedules of available action plans for eradication, so that any such insect can engender a rapid and organised response if it is detected, even though a range of taxa may possibly be present and many constituent species are probably innocuous.

Australia is and likely to remain one of the most quarantine-conscious countries in the world. Even before the principles involved were well understood, concern over the introduction of human diseases (especially typhus, transmitted by human lice) led to suggestions of fumigation using nitrous oxide to prevent and destroy 'contagion' in ships being advocated as early as 1799 (Goldsmit, 1984, 1988). This principle has since been developed into a scientific routine.

Australia was the first country to apply quarantine measures to aircraft arriving in the country, and in 1920 formally included aircraft within the definition of vessel. Since the 1930s, the arrival and survival of insects on aircraft has been studied progressively, with major emphasis on detecting possible disease vectors and ways of obviating this. The history of this development (Russell *et al.*, 1984) showed that monitoring of insects started with an order by the Director General of Health in Darwin in 1937 that every aircraft arriving at the airport or nearby flying-boat base from overseas be inspected and any insects found collected for identification. The first insect captured was a male *Anopheles* mosquito, and the taxa recorded from 1938–1979 (Tables 8, 9) included a number which had potential importance as disease vectors. Introduction of disease has always been a major concern of quarantine in Australia (Goldsmit, 1988). The presence of insects on aircraft was not novel by the 1940s: the Graf Zeppelin dirigible inadvertently carried insects on its transatlantic flight in 1928 and Laird (1984) noted experiments in 1803 investigating whether butterflies could survive balloon ascents.

Table 8. Summary of insect collections from aircraft arriving from overseas in Darwin (Northern Territory) between December 1938 and October 1941. Data abstracted from Russell *et al.* (1984).

Dates	No. aircraft	No. insects recovered	Mean no. insects/plane
Dec. 1938–Aug. 1939	177	481	2.7
Sept. 1939–Oct. 1941	337	291 (205 alive)	0.9
Taxa of public health interest			
Diptera:	Culicidae (9 spp.) Tabanidae Tachinidae Hippoboscidae	Ceratopogonidae Muscidae (3 spp.) Phoridae	Psychodidae Calliphoridae Chloropidae
Siphonaptera			
Blattodea			

Table 9. Mosquitoes which are disease vectors collected from aircraft in Australia from 1974–1979. Four (*Aedes vigilax, Culex quinquefasciatus, C. annulirostris, Mansonia uniformis*) are known as Australian species. After Russell *et al.* (1984).

Species	Diseases vectored	Collecting site
Aedes albopictus	Dengue fever, DHF, Chikungunya virus	Darwin, Perth
A. vigilax	RRV, Edge Hill virus, Sindbis virus	Darwin, Brisbane, Sydney
Culex quinquefasciatus	Bancroftian filariasis, Arboviruses	Darwin, Perth, Brisbane, Sydney
C. tritaeniorhynchus	JE, Chikungunya virus, Sindbis virus, Getah virus, Tembusu virus	Darwin, Sydney
C. gelidus	JE, Getah virus, Chikungunya virus, Sindbis virus, Tembusu virus	Darwin, Sydney
C. annulirostris	RRV, Kunjin, Australian encephalitis, Sindbis virus	Darwin, Brisbane, Sydney, Perth
Mansonia uniformis	Malayan filariasis, Bancroftian filariasis Chikungunya virus	Darwin, Brisbane, Sydney, Perth
Anopheles subpictus	Malaria	Darwin
A. sundaicus	Malaria	Darwin

The ability of many insects to survive long aircraft flights is well established, and most attention therefore has been paid to how to kill them on planes and how to prevent establishment of any survivors.

'Disinsection' of aircraft by spraying was recommended in Australia in the early 1930s (Cumpston, 1933) as one of two main quarantine strategies to prevent ingress of exotic species or individuals. The other main strategy involved airport sanitation, so as to restrict conditions suitable for establishment of arrivals, and surveillance to detect introductions. In particular, drainage of small ponds or swamps which could facilitate establishment of mosquitoes was recommended.

Many insects, even today, arrive alive in Australia on aircraft, and in past years were able to do so even in unpressurised planes. Mosquitoes, houseflies and flour beetles caged in the wheel bays of a Boeing 747B on commercial routes from Asia to Australia survived well (Russell, 1987), and the speed and frequency of modern air travel renders it a potent mode of potential ingress for insects (Fig. 29). Loading of planes may take place at night, so that insects can be attracted by lights to enter planes from nearby breeding sites. Likewise, planes standing on the tarmac at foreign airports whilst refuelling can act as 'gigantic light traps to attract local insect populations' (Russell *et al.*, 1984).

Both the optimal chemical formulation and the timing and mode of application in planes have been studied extensively by trials involving monitoring insects caged in various places in commercial aircraft. The usual disinsection technique has been to release pesticides, most commonly aerosols and nowadays pyrethrin-based, into the aircraft at some time when the doors are closed for flight. Laird (1984) noted that spraying on landing tended to be unpopular with passengers because it was perceived to delay disembarkation.

WHO (1966) recommended three main options for the timing of disinsection, namely:

(1) spraying of the passenger cabin after the doors had been locked at embarkation but before take-off: 'blocks-away disinsection',
(2) spraying before take-off, with all luggage and freight loaded, but no passengers on board: 'on-ground disinsection', and
(3) use of a dichlorvos dispensing system for inflight disinsection—an option which was never adopted in practice because of adverse effects on aircraft fittings (Russell, 1987).

More recent WHO recommendations (1985) include specifications for aerosols and chemical formulation, and the following disinsection procedures: blocks-away; spraying on the ground after landing—'on-arrival disinsection'; and use of a residual insecticide.

The efficiency of these and other techniques has been discussed in considerable detail. Arguments against 'blocks-away' treatment have

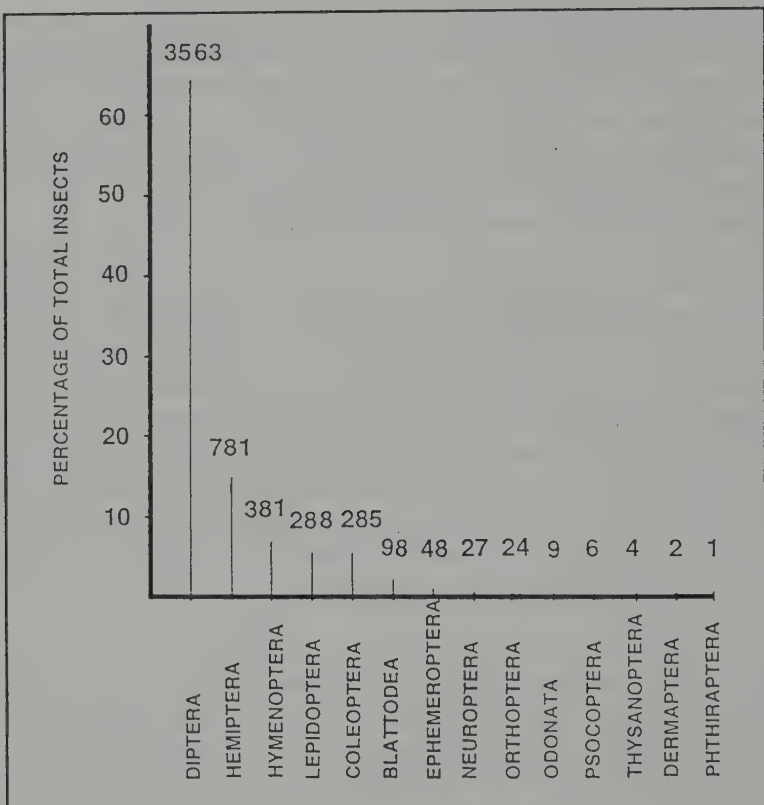

Fig. 29. Insects imported to Australia in aircraft: summary of relative representation of orders from 307 aircraft examined from 1974–1979. Data from Russell *et al.* (1984).

included the following: it is inefficient if done by the aircrew; any passengers who suffer an allergic reaction may not receive the most rapid and effective medical attention; and trained quarantine personnel are the best practitioners of disinsection. Until recently, in-flight spraying has been used little, partly on the grounds that the insecticide would be removed rapidly by air-conditioning systems. However, Russell and Paton (1989) found this not to be so for some formulations in Boeing 747 and 767 aircraft. 'Top-of-descent' disinsection is now recommended for all aircraft landing in Australia from overseas; the method was pioneered by Qantas and has now been adopted by many other countries. Areas such as toilets and flight deck, those not accessible for in-flight disinsection, were treated with a residual insecticide, permethrin. 'Top-of-descent' disinsection overcomes many of the objections raised by other systems: thus, because it occurs close to touchdown, any medical aid needed could be achieved quickly; it is not perceived as causing arrival or disembarkation delays;

and it is effective against insects which have entered the plane at intermediate ports-of-call and which would not be subject to blocks-away spraying.

The Australian Quarantine Inspection Service (AQIS) has legislative authority to exclude the entry of pests and diseases affecting plants and plant products and to respond to such exotic species by planning for arrival and attempting to eradicate them if they do arrive. As a result of finding dead adults of screwworm on a livestock vessel on its return to Victoria from Qatar in 1985 (Rajapaksa and Spradbery, 1989), AQIS instituted a programme to detect noxious exotic insects on livestock vessels returning from Asia and the Middle East, using electrocutor traps. Because of the enormous volume of goods arriving in Australia, and the number of sea and airports (37) and secondary arrival sites, complete investigation of incoming goods for exotic insects cannot be undertaken, and aspects of risk assessment are an integral part of quarantine inspection priorities. Risks are assessed on the kind of goods, their origin and the likelihood of any associated pests or diseases establishing in Australia (Navaratnam and Catley, 1986). These authors claim that too little attention has been paid in Australia to monitoring for introduced pests and measures for their eradication. Early eradication may be possible, as occurred for the giant African snail in Australia (Morschel 1983), but this contrasts with, for example, the European wasp (p. 90) for which Crosland (1991) showed that earlier recognition and attempts to eradicate it might have been feasible and would have saved the substantial costs which it now engenders.

Surveillance for exotic pests of crops in Australia is undertaken by the Department of Agriculture in each State and there is no monitoring at a national level. AQIS thus relies heavily on States for information on new pests, but there is now provision for rapid convention of a specialist Consultative Committee in the case of significant new pest arrivals. A meeting for warehouse beetle, *Trogoderma variabile*, in 1977 was one of the first such gatherings. In the same year, a similar meeting instituted rapid action to eradicate the giant African snail. The warehouse beetle was discovered in March 1977 in a rice mill in New South Wales, and other mills in the State were also found to have infestations in May 1977. Such restricted incidences may be amenable to rapid eradication.

Preparing for invaders

Despite continuing vigilance, other exotic pest insects will certainly make their way to Australia and some of these have the potential to cause immense damage. Some knowledge of the more likely serious entrants has

been accrued systematically in order to gain the ability to undertake a rapid strike response if they are detected, coupled with surveys to determine any such incidence. By far the most important of these is the old world screwworm fly, *Chrysomya bezziana*. This is discussed here in some detail to indicate the magnitude of concern such potential insect invaders can foster.

Screwworm fly. *Chrysomya bezziana* (Fig. 30) is a parasite of warm-blooded animals, predominantly mammals (including people) but also chickens, and the female fly must lay eggs (strike) in a wound in order for the life cycle to proceed. Such strikes give rise to larvae which can develop naturally only in living tissue. The maggots hatch within a day and may penetrate deeply into the host animal during their feeding period of around a week. Eggs are laid in masses of up to 250 around the edges of wounds and most females only produce one batch of eggs, although several may be possible.

Fig. 30. The old world screwworm fly, *Chrysomya bezziana*.

Losses caused by screwworm include lowering of meat and wool production, loss of breeding animals through sterility, and death of young stock due to navel-strike. Cattle may be struck on any body region where a wound or tick-bite facilitates entry, and these include the aftermaths of castration, dehorning or branding. Sterility can result from strikes to the

genital region. Unlike cattle, sheep may be struck at non-wound sites, especially in the infraorbital sinus. Wool loss can occur from staining and weak fleeces, and infestation of sheep would markedly exacerbate problems arising from blowfly strike.

The fly is widespread in Papua New Guinea and occurs through much of Asia and Africa. Its proximity to Australia has led to considerable investment in research orientated toward assuring the capability for rapid and efficient control should it reach this country. *Chrysomya bezziana* is regarded as the chief exotic disease threat to Australia (Australian Bureau of Animal Health, 1979) and biological work had been pursued by CSIRO in Port Moresby since 1973. If introduced, the screwworm could extend over much of northern Australia (Fig. 31), with a summer range (in favourable years) far into the south of the country. Economic loss to the cattle and sheep industries would be substantial, probably running into hundreds of millions of dollars, depending on prevailing commodity prices. It is highly unlikely that *C. bezziana* could extend into central Australia (Fig. 31) but it could probably thrive in the south-west if it were introduced there. The major initial impact would likely be on cattle in Cape York, and thereafter progressive invasion of cattle and sheep areas in Queensland and cattle stocks in the Northern Territory would be probable.

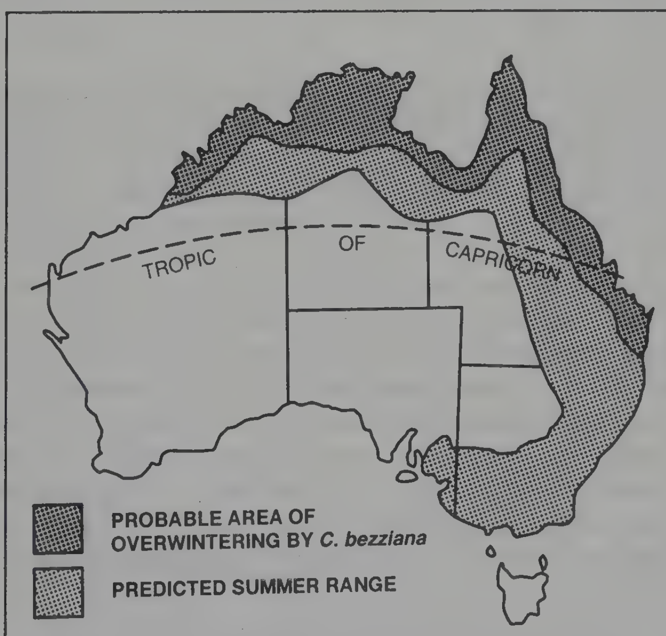

Fig. 31. Predicted spread of screwworm fly, *Chrysomya bezziana*, in Australia. After Australian Bureau of Animal Health (1979).

Monitoring the northern coastline of Australia is a formidable task and considerable thought has gone into considering how screwworm could arrive in Australia. In general, the likelihood of natural invasion by flight or on migratory birds or bats is believed to be remote. Torres Strait, with about 150 km between the closest parts of mainland Australia and Papua New Guinea, should constitute a barrier to such direct flight, but island-hopping (which would still involve distances of 50–60 km) may be possible. However, natural invasion could well have occurred by now if this were a likely option—but there is of course no **guarantee** that it will not occur in the future. Human-aided transport seems a much more likely occurrence. Many of the inhabited islands in Torres Strait support likely hosts of screwworm, either as domestic stock or feral populations, such as abandoned dogs. Movement of such animals between islands is regarded as the greatest possibility of spreading screwworm to Australia on ships. North to south transport is less common than in the other direction, although movement of deer is a specific and possibly important exception to this. Importation on pets (dogs, cats) smuggled into Australia to avoid the substantial quarantine period is also a threat. Animals from Indonesian fishing boats and the like could also be a danger, although a period at sea of more than a month may largely obviate this (Australian Bureau of Animal Health, 1979). Chances of arrival on aircraft are considered to be very low in relation to immigration on ships (Rajapaksa and Spradbery, 1989).

Cape York Peninsula is the most likely area for screwworm to arrive first in Australia, and the numbers of feral cattle there could facilitate establishment and render early detection difficult. For some years from 1976, a programme of 'sentinel cattle' was maintained in Bamaga on the far northern tip of Cape York. This consisted of small groups of cattle wounded with knife cuts and monitored for fly strike, but the method may be only an inefficient detection system and was replaced by the use of chemical attractant baits using a concoction termed 'Swormlure'. Traps could be employed cheaply on many sites on the mainland and on Torres Strait islands. Rather more drastic suggestions for preventing screwworm invasion included 'strategic destocking' of Torres Strait islands, with elimination of feral animals and greater degrees of control and monitoring of stock, combined with a discouragement of any new animal-based industries in the region. A buffer zone of northern Cape York was also proposed and involved a stock reduction of, especially, feral cattle and pigs, dingoes, and deer.

Such preventative steps might not work, of course, and methods for rapid and effective control if screwworm were ever detected in Australia also needed appraisal. The earlier example of a successful campaign against the New World Screwworm, *Cochliomyia hominivorax,* suggested

possible avenues for this—the main one being through use of sterile male flies. The strategy, which has been employed against some other dipterous pests, relies on the fact that the female flies normally mate only once. If sterilised males (mass-reared in captivity and sterilised by radiation) are released in sufficiently large numbers that they outnumber normal fertile males, females may mate with a sterile male and fail to produce offspring, so reducing the overall number of flies in the next generation. Repeated releases of sterile males to coincide with each field generation of flies leads to progressive reduction (and, hopefully, to eventual eradication) of the population. About 50 million sterile flies a week would be needed for a successful eradication campaign over an area the size of Cape York (Australian Bureau of Animal Health, 1979).

The most favoured of several options was to develop this method and potential in Papua New Guinea (within the extant range of screwworm) and work towards a facility which could then be 'mothballed' until or unless needed. A laboratory was established near Port Moresby for this purpose in 1973 and over the ensuing 18 years refined techniques for mass rearing screwworm without live hosts and for sterilising puparia by irradiation. The optimal conditions for release of sterile insects were also studied. The maintenance of a colony suitable for rapid increase to high production capacity developed progressively. A large scale field release in Papua New Guinea in 1982 was designed to evaluate the method. Results were very promising.

The Papua New Guinea laboratory has recently been closed and, although a replacement facility elsewhere in south-east Asia is regarded as highly desirable, its establishment is not yet certain to occur. Australia's 'first line of defence' against screwworm has thus been abandoned, at least for the present.

Banana skipper. The banana skipper butterfly, *Erionota thrax* (Hesperiidae), is another potential invader from the north. It has spread very rapidly through Papua New Guinea since it was recorded there in 1983 (Fig. 32; Sands *et al.*, 1991). The caterpillars feed on banana foliage and infestations result in reduced fruit yields once defoliation rises above about 20 per cent. It has thereby caused considerable concern in parts of Papua New Guinea where bananas are a staple food crop, and it has also reduced the supply of foliage used for traditional purposes (such as wrapping unripe fruit, basket-making, covering food). The strongly flying butterflies are crepuscular and attracted to light, so that they could possibly be attracted to boats. Their flight itself may be sufficient to facilitate island-hopping across Torres Strait onto Australia, with consequent damage in banana-growing areas of Queensland. Need for control in Papua New Guinea has stimulated a study of natural enemies, and both egg and larval parasitoids appear to be promising biocontrol agents.

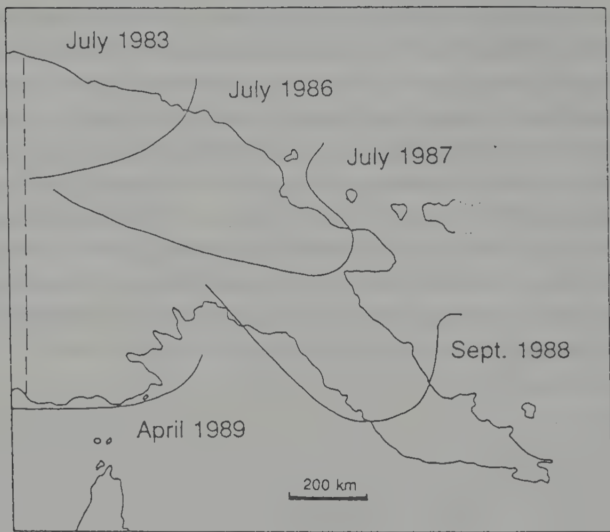

Fig. 32. The spread of the banana skipper butterfly, *Erionota thrax*, through Papua New Guinea. From Sands *et al.* (1991).

Russian wheat aphid. In contrast to such strongly-flying insects, relatively weak flyers such as some aphids are also anticipated immigrants to Australia. Arrival of the Russian wheat aphid, *Diuraphis noxia*, is regarded as inevitable, and, possibly, likely to occur very soon. It is a major pest of wheat and barley, and can cause death of young cereal plants and substantial yield loss from older ones. *Diuraphis* is highly dispersive and reached the Mediterranean region from its native western central Asia by the 1950s, South Africa by 1978, and the United States by 1985—where it caused substantial crop damage as soon as 1986.

This aphid could spread rapidly throughout the main grain growing areas of Australia and estimates (by CSIRO) of its damage potential range to several hundred million dollars annually. It is likely to arrive in aircraft. The drier inland parts of the Australian wheat belt would be particularly suitable for *D. noxia* as indicated by CLIMEX-matching studies (Hughes and Maywald, 1990; Hughes, 1988; Fig. 33).

A workshop held in 1988 to plan a campaign against *Diuraphis* in Australia identified three ways to prepare for countering it. All have been pursued actively since 1989. These were:

(1) to study the other species of aphids on wheat in Australia, to provide a base-line set of information against which additional impact could be assessed;

(2) to screen wheat varieties for resistance to the aphid. This work was undertaken in France and compared *Diuraphis* from several parts of its expanded range. Many traditional Australian wheat varieties are highly susceptible to *Diuraphis* and resistance may need to be increased substantially by utilising resistant varieties from elsewhere;

(3) the third approach is an unusual form of classical biological control which involved collection (in the aphid's native Russia) and release in Australia of a generalist wasp parasite of cereal aphids. Should the aphid arrive, a relevant and highly-adapted natural enemy would thus already be in place to help in its control.

It is patently impossible to prepare for all possible harmful arrivals in this way, but these examples demonstrate amply the concern which exotic species can foster. For many, an adequate response depends on early detection and recognition, which in turn depend on adequately trained personnel and the availability of good and easily used identification manuals for insects. In spite of all efforts to monitor any additional arrivals, the Australian fauna will certainly be subjected to further insect species arriving from other parts of the world, and the biological integrity of the island continent diminish even further as this occurs.

Fig. 33. Region of Australia indicated by CLIMEX-matching studies as favourable to Russian wheat aphid, *Diuraphis noxia*. After Hughes and Maywald (1990).

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INDEX

Exotic Insects in Australia

by T.R. New

This book discusses insects introduced by accident or on purpose to Australia: the so-called exotic insect fauna of Australia. The topic is important for many reasons, but especially because of the enormous economic impact that such introductions have had. Topics covered include background biological matters (arrival, establishment, invasion), beneficial species, pests and pest control, conservation issues and, finally, prediction and regulation. Examples include sheep blowflies, various insects of medical importance, dung beetles, woodwasps, aphids and others. Some important insects not yet present in Australia are also discussed.

The book will interest agricultural and medical scientists and all entomologists. Not least, it will interest all quarantine officers and remind them of their need to maintain vigilance. At educational institutions, it will be of interest and use both at undergraduate and graduate level.

Dr Tim New is one of Australia's leading entomologists. He is Reader in Zoology at La Trobe University, Melbourne. The author of several books and many scientific articles, he sits on a number of government committees as an adviser on entomological matters.

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